

Drosophilidae (Diptera) of Malawi

by

¹M.-T. Chassagnard, ^{1,2}L. Tsacas* and ¹D. Lachaise

(¹Lab. Populations, Génétique & Evolution, CNRS, 91198 Gif-sur-Yvette Cedex, France; ²Entomologie, Museum national d'Histoire Naturelle, 45 rue Buffon, 75005 Paris, France)

ABSTRACT

This paper, the first on the Drosophilidae of Malawi, records 76 species from the northern, central and southern parts of the country. These species belong to 11 genera comprising 14 subgenera, and 26 species groups (including 29 species subgroups). Keys are provided for *Amiota*, *Apenethecia*, the *Drosophila fima* group, *Liodrosophila* and *Mycodrosophila* species from Malawi. Sixteen new species are described: *Amiota bandai*, *Apenethecia argyrea*, *A. obscura*, *Drosophila adamisa*, *D. brachytarsa*, *D. seyanii*, *D. curta*, *D. dimitroides*, *D. neomitra*, *D. seguyiana*, *Lissocephala bergi*, *L. kamundii*, *L. sosefi*, *Mycodrosophila dudleyi*, *M. nigrans*, and *Scaptodrosophila melaena*. Five species are suspected to be new, but are left undescribed because of lack of material. Five of the fifteen species from Nyika are new. Thus, in spite of extensive *Brachystegia* woodland – not much suitable to Drosophilidae – it appears that the Malawian fauna is unexpectedly speciose. Although *Apenethecia capitata* was not found in Malawi, we redescribe it and include it in the key presented below; drawings are also given for *Lissocephala ambigua*, which was hitherto unfigured. New combination: *Drosophila lucida* Séguy, 1938 = *Liodrosophila lucida* (Séguy).

Some montane species of the *dentissima* group have non-overlapping geographical ranges in Malawi, between the Nyika and Vipha Plateau. The Nyika highlands would have more connections with the Western Border Range to the northwest of Lake Tanganyika, while the Vipha highlands would have more affinities with southern mountain ranges. Drosophilidae of the Nyika Plateau reveal also Madagascan and oriental links, and provide some interesting indices supporting the antiquity of the evergreen forest on the plateau. Most notably, a new species of the *robusta* group, *Drosophila seyanii*, represents the first afrotropical record of this mainly oriental (but also holarctic) species group.

A striking feature of the ecological relationships of African drosophilids is the consistency with which members of particular taxa (*Mycodrosophila* on fungus, *Apenethecia* on *Aloe*, *Lissocephala* on green figs, the *Drosophila fima* species group on red-black figs, or the *Scaptodrosophila aterrima* species group on Tubiflorales) use the same breeding substrate. Many such associations are documented in Malawi, and these are discussed.

INTRODUCTION

The drosophilid fauna of Malawi has so far been entirely unknown (Tsacas 1980a). Wheeler (1981 1986) did not mention any species from this country, which therefore has long constituted a gap in our knowledge of African Drosophilidae. Malawi was also lacking from a recent survey of southern African Drosophilidae (Tsacas 1990). As a result, all species mentioned in the present work are new to Malawi, and this greatly advances our knowledge of southern African Drosophilidae. In 1991, one of us (D. L.) used the opportunity of attending the 13th Congress of AETFAT (Association for the Taxonomic Study of the Flora of Tropical Africa) in Zomba, Malawi, to perform a four week field study on plant-insect relationships there, with a

*To whom correspondence should be addressed.

special focus on Drosophilidae, and more especially the fig-breeding species. This material is the basis of the present study. Of a total of 76 species collected, 16 are newly described here, and five more are recognised as new but left described because of insufficient material. This indicates how rich the Malawian fauna of Drosophilidae evidently is, and the need for more research. Major areas in Malawi like Mt Mulanje (up to 3000 m) are still unexplored in terms of their drosophilid fauna, and they are known to have a diversity of most suitable (for *Drosophila*) plant resources (Dowsett-Lemaire 1988, Chapman 1990).

DEPOSITORIES AND LOCALITIES

Depositories

Holotypes are deposited in the Museum national d'Histoire Naturelle, Paris (MNHN), paratypes in MNHN, the Natal Museum in Pietermaritzburg (NM), the Musée Royal de l'Afrique Centrale in Tervuren (MRAC), and the United States National Museum in Washington (USNM). Some 'further material examined' is from the South African Museum in Cape Town (S. A. Museum) and the Natal Museum (NM).

Collecting localities in Malawi, from south to north (Fig. 1)

1. *Zomba Plateau, Southern Region*, Zomba town, University of Malawi campus: Chancellor College, 790 m, April 3–11, 1991. At the northern end of the Shire Highlands lies the Zomba Plateau, a massif rising up almost sheer from the surrounding areas. Particular attention was paid to *Ficus sycomorus* var. *gnaphalocarpa* and *Ficus thonningii* var. *burcki* (Moraceae). (for phytogeographical description of the Zomba Plateau, see Dowsett-Lemaire 1989c: 93–96).
2. *Lake Malawi National Park, Cape Maclear, Southern Region*, March 30, April 1–2. Southern end of Lake Malawi; sandy, rocky and marshy shorelines; rocky islands, the largest of which is mostly steep-sided and wooded; steep, wooded, rocky mainland hills; and, a flat marshy area. The vegetation is *Brachystegia* woodland, with some *Combretum*, *Acacia* woodland and many baobabs in most terrestrial areas. A drosophilid trap was placed on the eastern ridge of the Cape Maclear Peninsula, close to the 'Mwalawamphini' rock, in a dry ravine with *Ficus ingens* (Moraceae), fallen fruits of *Ochna* sp. (Ochnaceae), and Vitaceae. Of note was the abundance of *Ficus abutilifolia* and *F. glumosa* on rocky shoreline outcrops, and of *Ficus ingens*, *F. bussei*, *F. bubu*, *F. sansibarica* and *F. ottoniifolia* ssp. *ulugurensis* on sandy shorelines.
3. *Lilongwe, Central Region*, 1000 m, March 23; April 19–20, 1991. The Lilongwe Plain, including the Lilongwe Nature Sanctuary, which is a *Combretum/Piliostigma* woodland. Of note was a patch of fruiting *Ficus thonningii* near the trapping site.
4. *Kasungu National Park, Central Region*, 1040 m, March 26–28; April 18–19, 1991. The Kasungu Reserve lies in Central Malawi on the Central African

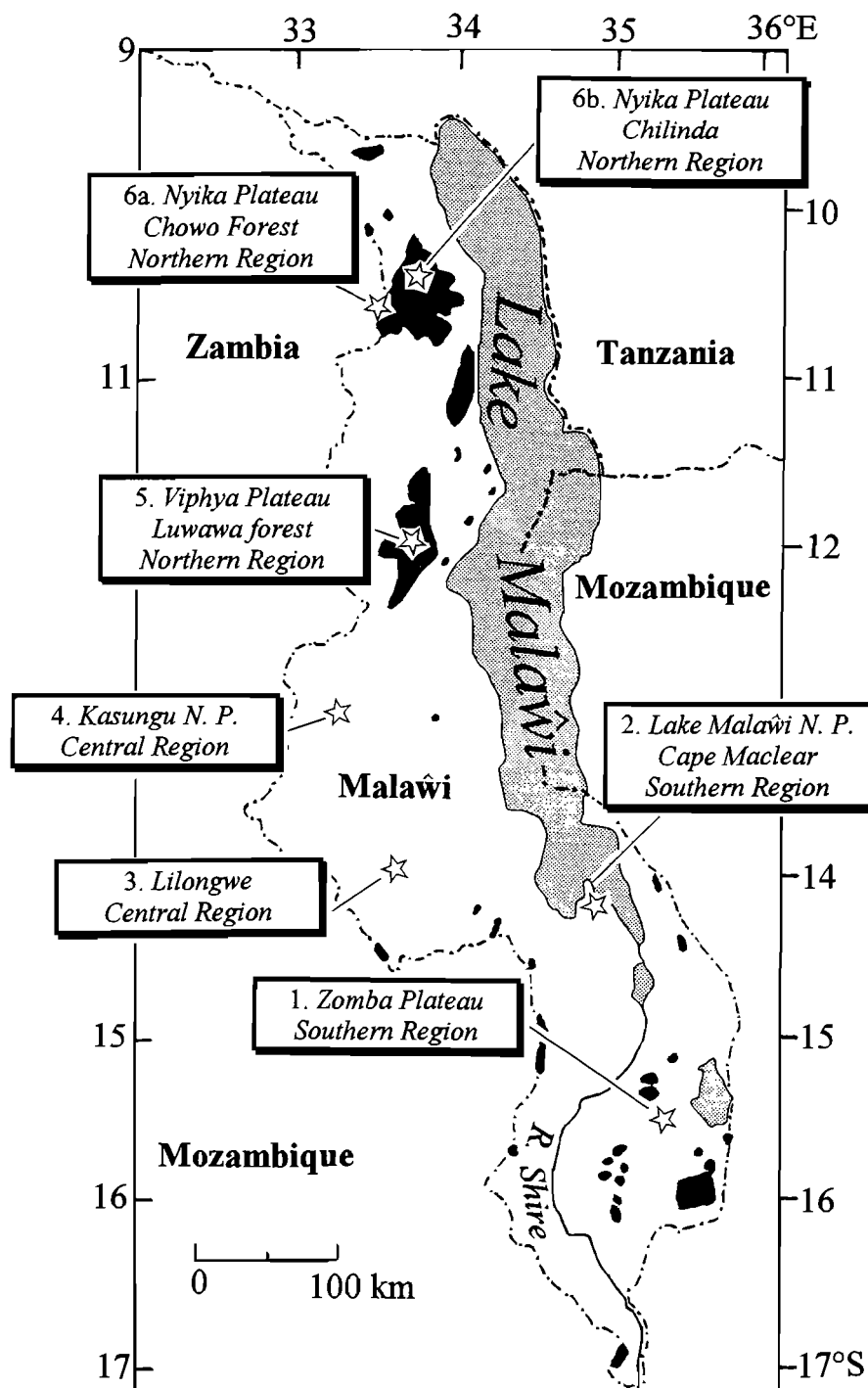


Fig. 1. Map of Malawi showing the collecting localities of *Drosophilidae*.

Plateau, along the western border with Zambia. It has a flat to undulating topography dissected by broad drainage lines ('dambos'), and a few isolated inselbergs particularly in the west. Its vegetation in the plateau area is basically a *Brachystegia* woodland (*Brachystegia stipula* and *Isoberlinia angolensis*), *Ficus thonningii* strangler on *F. sycomorus* (Moraceae), *Kigelia africana* (Bignoniaceae), *Acacia abbreviata* (Mimosoideae). Grassy dambos yield orchids and a diversity of other wild flowers, and open woodlands of *Pericopsis*, *Combretum*, *Albizia*, *Acacia*, *Piliostigma*, and *Terminalia* along the valleys of the major drainage lines. Inselbergs, especially 'Black Rock' are rocky outcrops supporting *Ficus glumosa* (Moraceae), *Sterculia quinqueloba* (Sterculiaceae), *Striga asiatica* (Scrophulariaceae), *Monotes engleri* (Dipterocarpaceae), *Euphorbia* sp. (Euphorbiaceae). Edge of Lifupa Lodge Dam with flowering *Hibiscus panduriformis*.

5. *Viphya Plateau, Northern Region*, 1500 m, March 28–30; April 12–13, 1991. Luwawa forest Reserve, Luwawa Pond, Luwawa Rest House, 1500 m, Viphya Plantation Division; non-indigeneous planted species, mostly *Pinus partula*, *P. eliotii*, *Cupressus* spp., *Eucalyptus* spp., *Colocasia antiquorum*; nearby is *Brachystegia* woodland including *Brachystegia taxifolia*, *Isoberlinia stoltzii*, *Uapaca kirkiana* (see Dowsett-Lemaire 1989c).
6. *Nyika Plateau, Northern Region*, April 14–17, mostly 2100–2500 m. Chowo Forest (90 ha), dark patch of evergreen forest on Malaŵi-Zambia border, 2140 m, 14–15 April 1991. Chilinda pine plantation Rest House near dams constructed during forestry operations, 2250 m, 15–16 April 1991. There is a high annual rainfall on the plateau (1200 mm at Chilinda) (see Dowsett-Lemaire 1985 1989c). The Nyika is the most extensive high plateau, not only in Malaŵi, but in all of south-central Africa, with an area of some 1800 km² above the 1800 m contour, which usually marks the zone of transition from woodland to montane grassland and forest. It lies between about 10°15'–10°50'S and 33°35'–34°05'E. Most of it is in Malaŵi, with a salient in Zambian territory – about 70 km² – on the western side (see Dowsett-Lemaire 1985 1989c for vegetation cover, and Meadows 1984 for geomorphology).

The rolling high plateau has a gently undulating topography. It is only on the edges of the plateau that steep, craggy escarpments occur, covered with *Brachystegia* woodland (*Brachystegia spiciformis*) and protea/heath scrub. Once clear of the *Brachystegia* woodland and *Protea* scrub, *Protea angolensis* var. *divaricata*, and *P. petiolaris*, the rolling short montane grasslands have the atmosphere of a Scottish moor: bracken on the freely draining slopes; lichen-covered rocks; mosses and ferns at the heads of valleys, in which grow small, dark patches of evergreen forests (Carter 1987). Two forests on the south of the plateau are dominated by *Juniperus procera* Hochst. ex Endl., which is at the southern limit of its natural range there. The Nyika Plateau is also one of southernmost extensions of giant *Lobelia mildbraedii* Engl. (Campanulaceae). Of special significance for drosophilids are *Ficus* spp. (Moraceae), *Aloe* spp. (Liliaceae), and *Uapaca*

kirkiana, *Canthium crassum*, *Gardenia jovis-tonantis* (Rubiaceae), of which the flowers or fruits provide potential breeding sites.

TAXONOMY

Family Drosophilidae

Subfamily Steganinae

Genus *Amiota* Loew, 1862

Amiota is poorly represented in the Afrotropical Region, where only the subgenera *Amiota* and *Phortica* are presently recorded.

Subgenus *Amiota*

The subgenus *Amiota s. str.* is poorly represented in the Afrotropical Region, with only three species including *A. bandai* here described. They can be recognised using the following key:

- 1 Scutum with 3 longitudinal, silvery pollinose bands **melanoleuca** Tsacas
- Scutum without bands 2
- 2 Mid legs with tibiae and two-thirds of femora dark brown **perpusilla** (Walker)
- Mid legs entirely yellowish **bandai** sp. n.

1) *Amiota (Amiota) bandai* Chassagnard & Tsacas, sp. n.

Figs 2–4

Diagnosis. Entirely black, grey-white spotted on head and thorax. Differs from *melanoleuca* Tsacas mainly by the lack of longitudinal bands on the scutum and from *perpusilla* (Walker) by mid legs being entirely yellow.

Male:

Head. Black with large band of whitish-grey on lower frons and face; facial carina very short and weakly developed. Antenna: pedicel reddish, flagellum black, arista with 4 dorsal and two ventral rays plus terminal fork, all long. Gena short, entirely or partly yellowish pollinose.

Thorax. Glossy black; postpronotum whitish-grey, wing base concolorously spotted; 2 pairs dorsocentral setae arising close to each other, the anterior setae very short; acrostichal setulae in 12 rows and one pair of acrostichal setae; 2 long katepisternal setae, subequal. Legs yellowish. Wing greyish-hyaline, vein R_{4+5} sinuous and converging apically with M. Halter yellowish-white.

Abdomen. Shining black.

Terminalia. Epandrium small relative to aedeagus and associated structures which are well-developed, entirely pubescent and with long setae ventrally; cercus densely covered with short pollinosity and with numerous long setae over entire surface. Surstylus large, nearly triangular, bearing inferoventrally a row of 12 prenisetae which are long ventrally and with gradually decreasing length dorsally, ventral teeth more than three times as long as dorsal ones; surstylus also with 3 clusters of three fine, short setae: close to ventral edge, close to comb basis and recessed (extending to

dorsal apex) respectively. Aedeagus and associated structures with highly unusual and complex features, yet a small hypandrium and a very elongate aedeagal apodeme as in Fig. 4 can be recognised.

Female: Similar to male.

Length (in mm): *Male*. Body 2.5; wing 2.0. *Female*. Body 2.4; wing 2.2.

Material examined: MALAWI: Holotype ♂, Zomba, 790 m, iv.1991, sweeping above fallen figs of *Ficus sycomorus* (Lachaise) (MNHNP); Paratypes, 1♂1♀, *idem* (MNHNP); 1♂, *idem* (NM).

Distribution. Malaŵi.

Etymology. Species dedicated to Elias A. K. Banda, Botanist at the National Herbarium and Botanic Gardens, Zomba, Malaŵi.

Subgenus *Phortica* Schiner, 1862

Only six species of this subgenus are described from the Afrotropical Region: *africana* Malloch, *fenestrata* (Duda), *flavithorax* (Duda), *sempunctata* (Séguy), *sobodo* (Burla), and *vumbae* Tsacas, of which only the second is present in the Malaŵian material.

2) *Amiota* (*Phortica*) *fenestrata* (Duda, 1939)

Material examined: MALAWI: 3♂1♀, Ntchisi Forest Reserve, 1334Ac, Montane forest & woodland, 3–4.xii.1980 (Londt & Stuckenberg) (NM); 1♂♀, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991; 1♀, Kasungu National Park, 28.iii.1991 (Lachaise) (MNHNP).

Distribution. South Africa; Uganda; Mozambique, Malaŵi (new record).

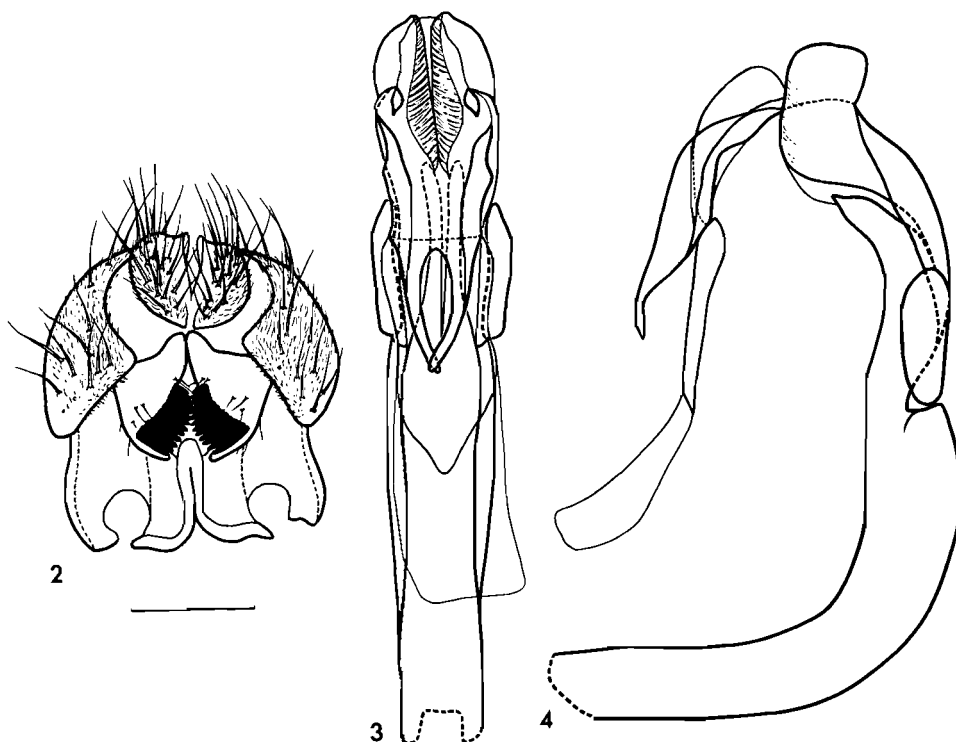
Genus *Apenthecia* Tsacas, 1983

Apenthecia is divided into two subgenera, *Apenthecia* and *Parapenthecia* Toda & Peng, 1992. The former subgenus is solely African where it is seemingly endemic; it comprises 10 species including the 2 new species here described.

Subgenus *Apenthecia*

The two new species of the subgenus can readily be included in the key of Tsacas (1983), which was re-used by McEvey *et al.* (1988). *Apenthecia capitata* (Collart, 1937) is not included in the following key.

- 1 Posterior reclinate orbital seta as short as the anterior one and scale-like or more or less thickened. African species.....Subgenus **Apenthecia** Tsacas.....2
- Anterior and posterior reclinate orbital setae scale-like. Species from Micronesia and ChinaSubgenus **Parapenthecia** Toda & Peng
- 2 Submedian dark annulus of tibiae of mid and hind legs almost as long as third length of tibia (Figs 19–20 in McEvey *et al.* 1988); posterior reclinate orbital seta thickened but not scale-like.....3
- Submedian dark annulus of tibiae of mid and hind legs short, almost as long as width of tibiae (Figs 17–18 in McEvey *et al.* 1988); posterior reclinate orbital seta either scale-like or short and thickened.....4



Figs 2–4. *Amiota (Amiota) bandai* Chassagnard & Tsacas sp. n. 2. Epandrium and associated structures, caudal view. 3. Aedeagus and associated structures, ventral view. 4. *idem*, lateral view. Scale: 0.1 mm.

- 3 Frons rusty-brown, fronto-orbital plate grey pollinose, posterior reclinate orbital seta thickened and reclinate towards eye; yellow subdistal band of posterior tibiae shorter than dark distal band (terminalia in Tsacas 1983, Fig. 7)
latifascia Tsacas
- Frons pale reddish, fronto-orbital plate brownish pollinose, posterior reclinate orbital seta shorter, thickened and straight (terminalia in Tsacas, 1983, Fig. 2).....
ambigua Tsacas
- 4 Frons and face entirely covered with dense silvery pollinosity, less distinct in females; posterior reclinate orbital seta transformed into distinct scale5
- Frons and face with slight, incomplete pollinosity; posterior reclinate orbital seta either scale-like or thickened.....7
- 5 Scutellum brown, pale on posterior edge; subdistal yellow band of hind tibia as long as dark distal band (terminalia in Hackman 1960, Figs 4–5, and Tsacas 1983, Fig. 5).....**crassiseta** (Hackman)
- Scutellum rusty-brown; subdistal yellow band of hind tibia longer than dark distal band6
- 6 Scutum with 2 rusty longitudinal stripes, first tergite with brown median spot (terminalia in Tsacas 1983, Fig. 3)**argentata** Tsacas

- Scutum without rusty longitudinal stripes, first tergite without brown median spot. Terminalia as in Figs 5–9 **argyrea** sp. n.
- 7 Scutellum brown, with yellow fringe on posterior edge not beyond base of apical scutellar setae; posterior reclinate orbital seta only thickened, shorter than anterior reclinate orbital 8
- Scutellum paler distally, without well-marked yellow border, posterior reclinate orbital scale-like 9
- 8 Scutum dark (almost black), yellowish pollinose; femur black more or less yellow apically (terminalia in Tsacas 1983, Fig. 4) **brincki** (Hackman)
- Scutum black without pollinosity; femur black, slightly paler on fore femur, narrow yellow apical area on hind tibia (terminalia, Figs 10–13) **obscura** sp. n.
- 9 Scutum with 5 brown, interrupted bands, anepisternum brown banded; brown band of tergites large and straight (terminalia in Tsacas 1983, Fig. 8) **vittata** Tsacas
- Scutum with 3 brown narrower interrupted bands, anepisternum not brown banded; brown band of tergites slightly incurved and narrower (terminalia in Tsacas 1983, Fig. 6) **imperfecta** Tsacas

The two species described below can be distinguished from *A. capitata* (Collart) and *A. argyrea* notably by the densely pollinose head and coxa, and from *A. obscura* by leaf-like *or3*, frontal colouration, and tergal pattern.

3) *Apenthecia* (*Apenthecia*) *argyrea* Chassagnard & Tsacas, sp. n.

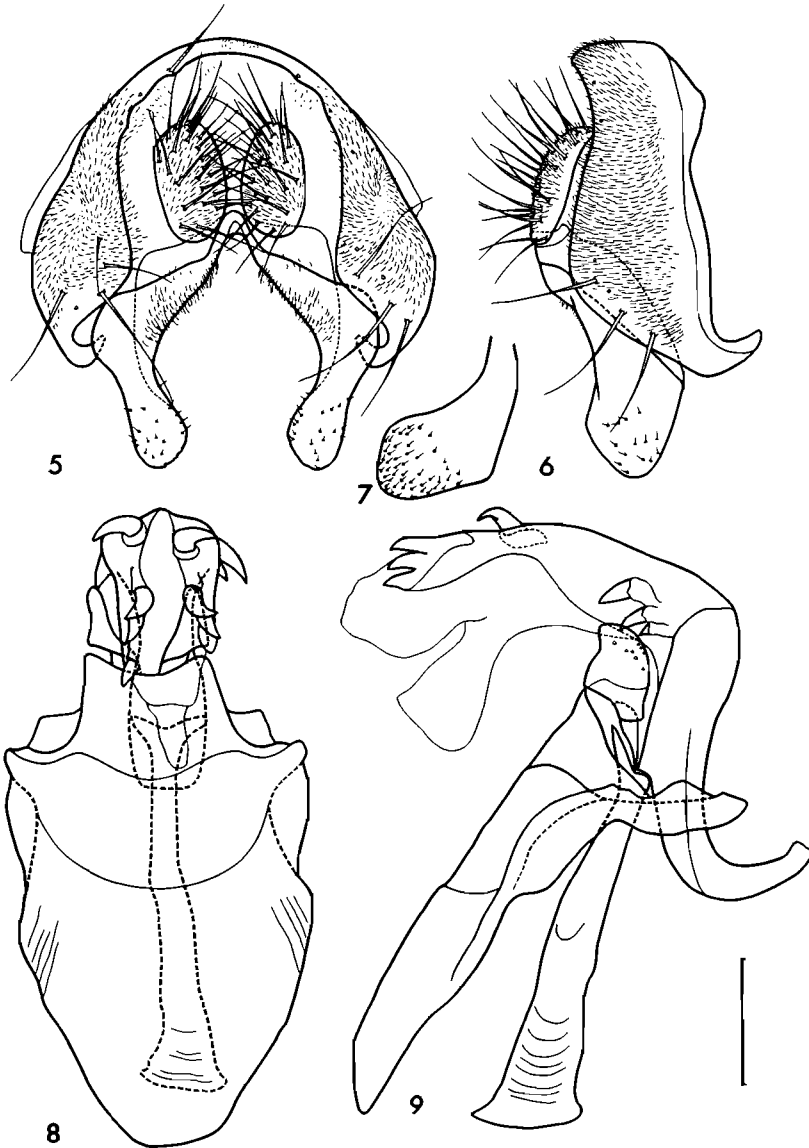
Figs 5–9

Diagnosis. Characterised by dense silvery pollinosity of head and fore coxa, characters which put it closer to *A. argentata* Tsacas, the distinguishing characters being mainly in the male terminalia.

Male:

Head. Frons, face, gena and eye outline covered with dense silvery pollinosity, basic colour of frons yellow-brown anteriorly and brown-bronze posteriorly. Ocellar triangle and fronto-orbital plate greyish-brown, orbital seta anterior *or1* proclinate, anterior reclinate orbital seta *or2* long and arising closer to *or1* than to posterior reclinate orbital seta *or3*, *or3* scale-like. Facial carina not much prominent, enlarged apically with brown, non-pollinose, half-moon patch at the very apical end. Brown clypeus, palpus yellowish apically. Antenna brownish-yellow, arista bare. Eye dull brick.

Thorax. Scutum rusty-brown, greyish pollinose. Eight rows of acrostichal setulae, two pairs dorsocentral setae (lacking on holotype), arising backwards, the anterior markedly shorter than posterior ones. Scutellum and scutum concolorous, the former rusty apically, with one longitudinal band on proepimeron, another on anepisternum, and a third overlapping anepisternum and katepisternum. Two long katepisternal setae close to posterior border. Legs: fore leg: femur brown, tibia with 2 brown annuli, one apical and the other submedian and narrower, the yellow band inbetween



Figs 5–9. *Apenthecia (Apenthecia) argyrea* Chassagnard & Tsacas sp. n.. 5. Epandrium and associated structures, caudal view. 6. *idem*, lateral view. 7. Surstylus, internal view. 8. Hypandrium and associated structures, ventral view. 9. *idem*, lateral view. Scale: 0.1 mm.

almost as large as the apical annulus, tarsus yellow; mid leg: femur yellow, tibia as in fore leg, tarsus yellow; hind leg: femur brown turning paler apically, tibia as in fore and mid leg but yellow band between brown annuli significantly larger than apical annulus, tarsus yellow. Wing hyaline, veins brownish, R_{4+5} and M parallel apically; C-index = 2.3.

Abdomen. Tergites: T3 yellow with faint triangular median patch, 2 large brown

lateral patches and 2 antero-marginal elongated ones, brown laterally, T4–5 brown with one large pale anterior stripe not reaching lateral borders and two pale patches on postero-lateral angles, T6 brown with pale elongated patch anteriorly.

Terminalia. Epandrium entirely covered with short dense pubescence, caudally larger in its basal third, surstylus long and large laterally, densely spinulate apically more especially internally. Aedeagus with very unusual and complex structure, partly membranous and bearing numerous strong teeth.

Female: Similar to male but with less dense pollinosity on head and coxa. Abdomen with yellow areas of tergites slightly more extended, T7 entirely brown. Wing, C-index = 2.3.

Length (in mm): *Male.* Body 2.8; wing 2.2. *Female.* Body 2.8; wing 2.6.

Material examined: MALAWI: Holotype ♂, Zomba, 790 m, 10.iv.1991, sweeping above fallen figs of *Ficus sycomorus* (Lachaise) (MNHNP); Paratype ♀, *idem* (MNHNP).

Distribution. Malaŵi.

Etymology. From Greek, ἀργυρος, εα = silvery, referring to the dense silvery pollinosity of the head.

4) *Apenthecia* (*Apenthecia*) *obscura* Chassagnard & Tsacas, sp. n.

Figs 10–13

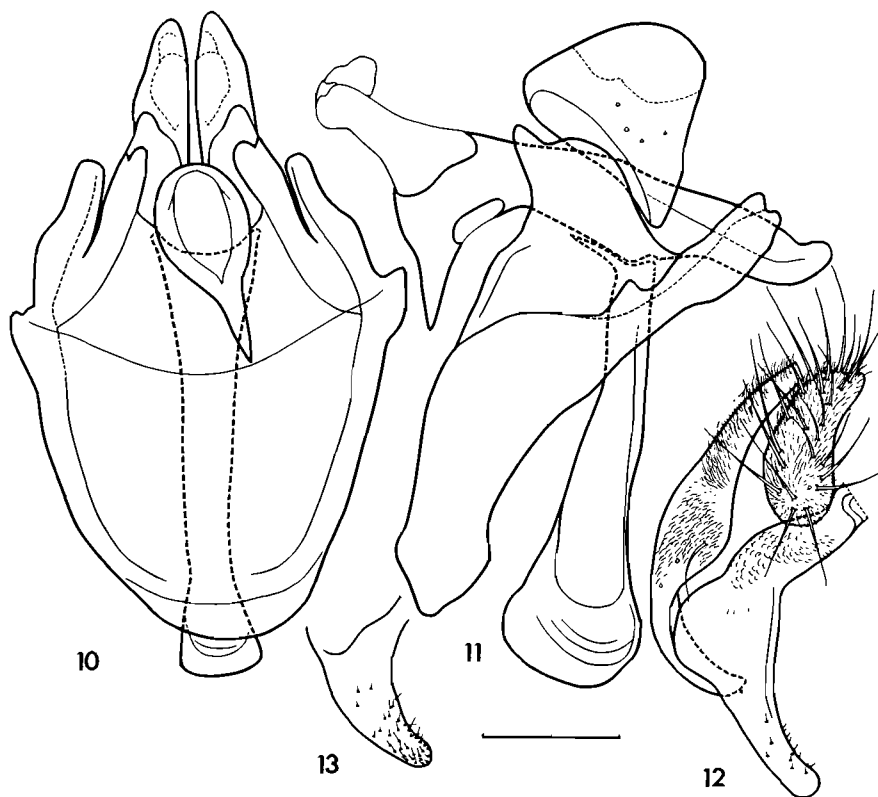
Diagnosis. Dark and dull, posterior reclinate orbital seta short and flattened. Surstylus long and distiphallus large.

Male:

Head. Frons bronze-brown darkened anteriorly, turning black at level of ocellar triangle and entirely covered with faint greyish pollinosity visible from some angles. Ocellar triangle and fronto-orbital plate brown with faint greyish pollinosity. *or1* long-curved medially, *or2* developed and long, *or3* short and flattened. Postocellar setae very short and convergent. Face brown, covered with faint greyish pollinosity, denser and whitish in the subantennal fossae, facial carina finely chiselled and apically enlarged. Antenna: pedicel rusty with one dorsal seta, flagellum brown but rusty and greyish pollinose basally, arista bare. Eye well-developed, rusty or brown depending upon angle of observation.

Thorax. Scutum dark brown, non uniform with either reddish pollinose (anteriorly) or glossy patches. Scutum damaged, thus counting of rows of acrostichal setulae impossible, and presence of anterior dorsocentral setae conjectural; scutellum concolorous with scutum, and with small yellowish apical spot. Pleura brown, greyish pollinose yet with 3 bare stripes, the 2 superior on anepisternum and joined anteriorly, the inferior encroaching on anepimeron posteriorly, the third larger overlapping the anepisterno-katepisternal suture. Two long katepisternal setae arising close to each other, almost equal and with tip reclinate toward body. Legs with coxa and femur brown, fore tibia with subapical yellow band as long as apical brown band, the remaining brown more extensive and occupying slightly less than half tibial length. Mid and hind tibiae with bands similarly arranged as on fore tibiae but with apical brown and yellow median bands more extensive, and brown basal annulus

short, revealing large pale area at extreme base. Wing hyaline, veins thinly darkened, C-index = 2.3.



Figs 10–13. *Apenthecia (Apenthecia) obscura* Chassagnard & Tsacas sp. n. 10. Hypandrium and associated structures, ventral view. 11. *idem*, lateral view. 12. Epandrium and associated structures, caudal view. 13. Surstylus, internal view. Scale: 0.1 mm.

Abdomen. Brown except T1 paler and T2 and T3 with a narrow pale basal stripe accompanied by 2 concolorous lateral patches.

Terminalia. Epandrium pubescent except on ventral epandrial expansion, extremities tapering, surstylus very long, slender, densely spinulate mostly internally. Aedeagus and associated structures with complex structure, aedeagus short, distiphallus appears like a miner's pick pointing anteriorly.

Female: Unknown.

Length (in mm): Male. Body 2.9; wing 3.1.

Material examined: MALAWI: Holotype ♂ (unique), Nyika-Chilinda, 2250 m, 15–16.iv.1991 (Lachaise) (MNHNP).

Distribution. Malawi.

Taxonomy. Species close to *Apenthecia latifascia* Tsacas in male terminalia, differing principally by almost entirely brown abdomen.

Etymology. From Latin, the name referring to the overall dark appearance of the holotype.

Apenthecia (Apenthecia) capitata (Collart, 1937)

Figs 14–15

Amiota capitata Collart, 1937: 121 (picture of head, facial view).

Although *A. capitata* was not found in Malaŵi, we redescribe the species to include it in the above key.

Female:

Head. Frons ground colour brownish-yellow, paler anteriorly, covered with silvery pollinosity less dense than in *argyrea*, denser on fronto-orbital plates; orbital setae: *or1* distant and *or2* and *or3* still more distant from eye margin, *or2* closer to *or1* than to *or3*, the latter scale-like and tapering apically; ocellar triangle blackish, surrounded by denser pollinosity than on remainder of frons; outer vertical seta short and convergent; face ground colour brown, pollinosity grey, yellowish on wide epistoma, facial carina not much prominent, very wide just below antennal insertions and narrowing gradually toward apex, interrupted before epistoma. Clypeus blackish, silver pollinose. Palpus yellow with sparse silvery pollinosity and 4 setulae ventrally. Antenna (only one preserved, detached from fly: pedicel yellowish, flagellum rounded, ground colour brown, slightly silver pollinose, arista pubescent.

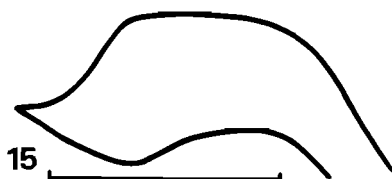
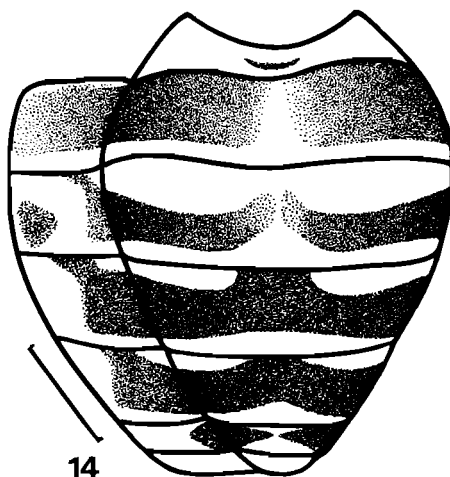
Thorax. Scutum ground colour brown, with sparse grey-yellowish pollinosity, just inbetween 2 rows of dorsocentral setae are 2 short rusty bands; posterior dorsocentral setae twice as long as anterior ones; 3 last acrostichal setae long; scutellum light-brown with yellow longitudinal band concolorous with scutellum edges medially, basal scutellar setae divergent, apical scutellar setae crossed. Fore leg: femur brown with a narrow zone paler anteriorly, a row of 10 short posterior setae; tibiae yellow with a distal brown annulus hardly larger than tibial width, and a second brown, similarly wide (less wide anteriorly) annulus submedially; tarsus yellow. Mid leg: coxa yellow; femur yellow with basal brownish annulus twice as large as femur width; tibia as fore tibia, the yellow space between distal and median brown annulus almost as large as distal annulus; tarsus yellow. Hind leg: coxa yellow; femur as mid femur; tibia with distal annulus brown as on mid leg, and a second one similarly brown but more basal than on fore and mid legs, the yellow space between two brown annuli 1.5 times width of distal annulus.

Abdomen. As in Fig. 14.

Length (in mm): Female. Body 2.4; wing 2.8.

Material examined: Holotype ♀ with following labels: 1. red label, TYPE (printed)/ *A. capitata* (handwritten); 2. white label, MUSEE DU CONGO/Park Albert (printed): Chumbi (handwritten)/XI.1933/Dr De Wulf (printed); 3. white label, Collart det. (printed)/*Amiota capitata* m. (handwritten); 4. white label, R. DET./♀ ♀ /3252 (printed); 5. white label, *Apenthecia/capitata* (Collart)/L. Tsacas & M.T. Chassagnard/1994 (handwritten) (MRAC).

Distribution. Eastern Zaïre; known only from unique female holotype.



Figs 14–15. *Apenthecia (Apenthecia) capitata* (Collart). 14. Abdomen. 15. Posterior, scale-like, reclinate orbital seta. Scale: 0.1 mm.

Genus *Leucophenga* Mik, 1886

Although solely represented by the subgenus *Leucophenga s. str.* in Africa, the genus *Leucophenga* is nonetheless the second most speciose genus after *Drosophila*. In the Malawian collection 11 species can be recognised, but only three can be named. The eight others are represented by unique females or males, and identification of African species of *Leucophenga* from limited material remains controversial. This is due to exceptional taxonomic complexity (especially inherent to polychromatic sexual dimorphism) and variability effecting the mesonotum, scutellum and abdomen. This presumably explains why no new species has been described since Bächli's (1971) monograph devoted to African *Leucophenga*, and Tsacas' (1972) revision of Adams' (1905) types.

Subgenus *Leucophenga*

flavopuncta group Bächli, 1971

5) *Leucophenga* sp. A

Material examined: MALAWI: 1♂2♀, Zomba, 790 m, 6.iv.1991, sweeping above fallen figs of *Ficus sycomorus* (Lachaise) (MNHNP).

6) *Leucophenga* sp. B

Material examined: MALAWI: 1 ♀, Zomba, 790 m, 8.iv.1991, above fallen figs of *Ficus thonningii* (Lachaise) (MNHNP).

mutabilis group Bächli, 19717) *Leucophenga* sp. C

Material examined: MALAWI: 1 ♀, Viphya Plateau, Luwawa, *Pinus* spp. forest, 1500 m, 29.iii.1991. MALAWI-ZAMBIA: 1 ♀, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP).

8) *Leucophenga* sp. D

Material examined: MALAWI: 1 ♀, Zomba, Chancellor College, 790 m, 5.iv.1991, sweeping above fallen figs of *Ficus thonningii* (Lachaise) (MNHNP).

9) *Leucophenga* sp. E

Material examined: MALAWI: 1 unsexed, Zomba, Chancellor College, 790 m, 8.iv.1991, sweeping above fallen figs of *Ficus sycomorus* (Lachaise) (MNHNP).

proxima group Bächli, 197110) *Leucophenga mansura* (Adams, 1905)

Material examined: MALAWI: 1 ♂, Zomba, Chancellor College, 790 m, 8.iv. 1991, above fallen figs of *Ficus thonningii* (Lachaise) (MNHNP).

Distribution. Zimbabwe; Ethiopia, Ivory Coast, Zaïre, Uganda, South Africa, Malaŵi (new record).

11) *Leucophenga proxima* (Adams, 1905)

Material examined: MALAWI: 2 ♂, Viphya Plateau, Luwawa Forest Reserve, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Zimbabwe, Zaïre, Uganda, Ivory Coast, Chad, South Africa (Kwazulu-Natal), Malaŵi (new record).

12) *Leucophenga* sp. F

Material examined: MALAWI-ZAMBIA: 1 ♂, 3 ♀, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP).

These 4 specimens undeniably constitute a new species which we nonetheless leave undescribed because of lack of sufficient material.

13) *Leucophenga* sp. G

Material examined: MALAWI: 1 ♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

This is undoubtedly a new species which we nonetheless leave undescribed because of insufficient material.

14) *Leucophenga* sp. H

Material examined: MALAWI: 1♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP). This male undoubtedly represents a new species, which we nonetheless leave undescribed for lack of sufficient material.

subpollinosa group Bächli, 197115) *Leucophenga subpollinosa* (de Meijere, 1914)

Material examined: MALAWI: 2♂2♀, Zomba, 790 m, above fallen figs of *Ficus thonningii*, 10.iv.1991; 1♀, *idem* but 5.iv.1991; 1♀, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Indonesia (Java), Taiwan, Japan, Nepal, Micronesia; Sri Lanka; Eritrea, Nigeria, South Africa, Malawi (new record).

Comments. The species status of this taxon, widespread over the Afrotropical, Oriental and Australasian biogeographic regions, is questionable. Though descriptions are quite consistent, figures of the male terminalia of specimens from Nepal published by Okada (1966), and from Micronesia by Wheeler & Takada (1964) are inconsistent with one another and Malawian specimens. Okada (*loc. cit.*) noticed some differences in terminalia according to whether the relevant males originated from Nepal or Japan. Bächli (1971), who examined specimens from all the above-mentioned regions, expected a complex of species to exist under this name. Without conclusive evidence, we consider the specimens from Malawi as conspecific with *L. subpollinosa*.

Genus *Stegana* Meigen, 1830

Within the present Malawian collection, only the subgenus *Steganina* is represented, including females only of two unidentified species. Of the eight African species, seven can be identified using Tsacas & Chassagnard's (1996) key. The eighth species, *Stegana (Steganina) ikedai* – recorded from Ethiopia – was omitted from Tsacas & Chassagnard's (1996) paper.

Subgenus *Steganina* Wheeler, 196016) *Stegana (Steganina)* sp. A

Material examined: MALAWI: 1♀, Zomba Plateau, Chancellor College, sweeping above fallen figs of *Ficus thonningii*, 5.iv.1991 (Lachaise) (MNHNP).

17) *Stegana (Steganina)* sp. B

Material examined: MALAWI: 1♀, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500, 29.iii.1991 (Lachaise) (MNHNP).

This species is characterised by the entirely black abdomen.

Subfamily Drosophilinae

Genus *Drosophila* Fallén, 1823

Within the exceedingly large genus *Drosophila*, the content and limits of which are

presently changing, three subgenera are represented in the Malaŵian collection, namely *Drosophila*, *Dorsilopha* and *Sophophora*. Following Grimaldi's (1990) classification, *Hirtodrosophila* and *Scaptodrosophila* are treated as separate genera.

Subgenus *Dorsilopha* Sturtevant, 1942

Out of the four species in this depauperate subgenus (Toda 1986), the cosmopolitan species *D. busckii* is found only in Malaŵi, within the Afrotropical Region.

18) *Drosophila (Dorsilopha) busckii* Coquillett, 1901

Material examined: MALAŴI: 1 ♀, Zomba Plateau, 790 m, above fallen figs of *Ficus sycomorus*, 6.iv.1991; 1 ♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991; 5 ♂, 3 ♀, Nyika Plateau, Chilinda, 2250 m, 15–16.iv.1991 (Lachaise) (MNHNP). A series of wild-caught females from Nyika-Chilinda, *idem*, were used as foundresses of 3 isofemale and 3 multifemale lines; 1 ♀ from Lilongwe, 1000 m, 20.iv.1991, was used to found one isofemale line.

Distribution. Cosmopolitan.

Subgenus *Drosophila* Fallén, 1823

This large subgenus has long been considered depauperate in the Afrotropical Region, compared to other biogeographic regions. Recent investigations, especially in East Africa, have shown that this assumption is, however, false. Presently the subgenus comprises 35 species including 8 cosmopolitan taxa (Tsacas & Chassagnard 1994), and there are many additional undescribed new species in our collections. In the Malaŵian material we found 11 species, including 2 cosmopolitan species, 2 unidentified species, and three new species which are here described.

immigrans group Sturtevant, 1942

immigrans subgroup Wilson *et al.*, 1971

19) *Drosophila (Drosophila) immigrans* Sturtevant, 1921

Material examined: MALAŴI: 2 ♀, Zomba Plateau, Chancellor College, above fallen figs of *Ficus thonningii*, 790 m, 3.iv.1991; 1 ♀, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 5 ♂, 3 ♀, Nyika Plateau Chilinda, 2250 m, 15–16.iv.1991 (Lachaise) (MNHNP); one female and a series of wild-caught females from Nyika-Chilinda were used as foundresses of one isofemale and one multifemale lines respectively.

Distribution. Cosmopolitan.

nasuta subgroup Wilson *et al.*, 1969

20) *Drosophila (Drosophila) nasuta* Lamb, 1914

Material examined: MALAŴI: 7 ♂, 2 ♀, Zomba, Chancellor College, 790 m, 5.iv.1991, above fallen figs of *Ficus thonningii* (Lachaise) (MNHNP).

Distribution. Seychelles, Togo, Benin, Nigeria, Cameroun, Congo, Zaïre, Kenya, Burundi, Madagascar, Réunion, Mauritius, Rodriguez, Brazil, Malaŵi (new record).

polychaeta group Sturtevant, 194221) *Drosophila (Drosophila) hirtipes* Lamb, 1914

A junior synonym of *hirtipes* is *iri* Burla, 1954 (Tsacas 1994).

Material examined: MALAWI: 1♂, Kasungu National Park, 28.iii.1991 (Lachaise) (MNHN).

Distribution. Seychelles; Ivory Coast, Benin, Nigeria, Cameroun, Gabon, Congo, Zaïre, Madagascar, Bioko (Fernando Po), Mauritius, Malaŵi (new locality).

repleta group Sturtevant, 1942

This group is solely represented in Africa by its cosmopolitan representatives *repleta*, *hydei* and *buzzatii*, the latter two being present in the Malaŵi sample.

22) *Drosophila (Drosophila) buzzatii* Patterson & Wheeler, 1942

Material examined: MALAWI: 1♂, Lilongwe, 20.iv.1991 (Lachaise) (MNHN). (identification C. R. Vilela).

Distribution. South America; Australia, North Africa, Europe, Senegal, Benin, South Africa, Réunion, Rodriguez, Malaŵi (new record).

23) *Drosophila (Drosophila) hydei* Sturtevant, 1921

Material examined: MALAWI: 1♂, locality not mentioned on label, xii.1973 (Feijen) (MNHN).

Distribution. Cosmopolitan, notably Madagascar, South Africa, Réunion, Seychelles, Kenya (new record), Malaŵi (new record).

robusta group Sturtevant, 1942

The new species described below is of major interest as it represents the first afrotropical record of a member of this basically oriental species group (a few species are nevertheless known in the Holarctic Region). This unexpected finding provides further evidence of relationships between the oriental and afrotropical drosophilid faunas. It is however difficult to explain how *D. seyanii* is related to *D. lacertosa* Okada, 1956, the seemingly closest Oriental relative, of which the geographic range includes some contact zones with the Palearctic Region (Korea, Nepal).

lacertosa subgroup Watabe & Nakata, 198924) *Drosophila (Drosophila) seyanii* Chassagnard & Tsacas, sp. n.

Figs 16–21

Diagnosis. Brown, large, faintly reminiscent of *D. hirtipes* Lamb (= *iri* Burla), but no affinities with any afrotropical species.

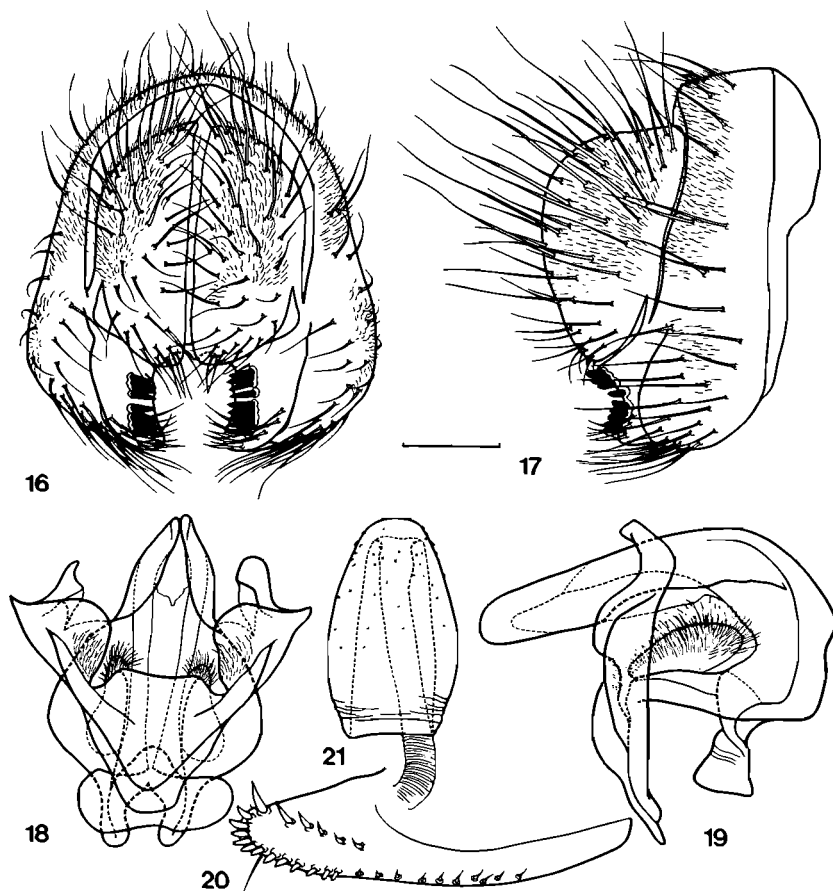
Male, Female:

Head. Frons brown, slightly velvet, sometimes revealing pale pollinosity in anterior view, paler anterior to fronto-orbital plate, this almost glossy black, widened anteriorly, orbital setae: *or1* markedly shorter than *or3*, *or2* short and thin, midway between the two others. Ocellar triangle concolorous with fronto-orbital plate, ocelli

reddish, postocellar setae well developed and indistinctly crossing. Face entirely brown, facial carina broad, also between antennae, flattened dorsally. Antenna: pedicel brownish, flagellum black, arista with 4 straight dorsal and 2 ventral rays plus terminal fork. Clypeus black, pale pollinose, especially on either sides. Palpus black, hirsute. Gena broad, non uniformly brown. One vibrissa. Eye dark dull brick.

Thorax. Scutum glossy brown. Dorsocentral setae arising close to each other, the anterior setae nearly half the length of the posterior setae. Acrostichal setulae irregular, in about 8 rows at level of anterior dorsocentral setae, 4 to 6 posteriorly. Scutellum brown, less glossy and smooth than scutum, basal and subapical scutellar setae subequal. Pleura glossy brown, here and there paler, 2 katepisternal setae, the anterior seta slightly shorter and thinner. Legs indistinctly brown. Wing brown, veins black, C-index, male = 3.1, female = 3.5. Halter faintly brown, contrasting with remainder of thorax.

Abdomen. Black with 2 yellowish paramedian anterior patches, half-moon shaped on three last tergites.



Figs 16–21. *Drosophila (Drosophila) seyanii* Chassagnard & Tsacas sp. n. 16. Epandrium and associated structures, caudal view. 17. *idem*, lateral view. 18. Hypandrium and associated structures, ventral view. 19. *idem*, lateral view. 20. Ovipositor. 21. Spermatheca. Scale: 0.1 mm.

Male terminalia. Epandrium relatively narrow, bearing row of irregular, long setae situated at mid-width, epandrial fragma narrow, slightly broader in its dorsal half, extending all along anterior border of epandrium. Posterior half of epandrium shortly pubescent. Ventral epandrial extension large and conspicuously rounded, bearing heavy setation, still denser at the apex. Cercus attached to epandrium, bulky, hirsute, cercal setae shorter and denser ventrally and especially ventromedially, shortly pubescent on dorsal two thirds. Surstylus with marginal row of 8–9 prensisetae, sometimes in 2 clusters; the comb concave in lateral view, and surrounded by numerous long and thin setae ventrally. Hypandrium with a complex structure, posterior border straight without paramedian setae, posterodorsal part of hypandrium twisted, anterior parameres ovoid and hirsute; posterior parameres slightly shorter than aedeagus, tapered distally, aedeagus long, strongly incurved at 90° ventrally, aedeagal apodeme short, bifid.

Female terminalia. Ovipositor narrow, elongate, tapered apically, bearing apically a row of 6 closely-set teeth, turning dorsally to a row of 6 teeth with declining size from apex to base, the former most robust, and followed anteriorly to long ventral seta by 6 shorter teeth and about 10 short spines. Spermatheca elongate and ovoid, coarsely spinulate.

Length (in mm): *Male.* Body 4.7; wing 4.0 mm. *Female.* Body 4.0; wing 3.7.

Material examined: MALAWI-ZAMBIA: Holotype ♂, Nyika Plateau, Chowo forest, 2120 m, 14.iv. 1991 (Lachaise); Paratypes, 1♂3♀, *idem* (MNHNP); 1♀, *idem* (NM).

Distribution. Malawi, Zambia. Although the Chowo forest is located on the Zambian side of the Nyika Plateau, it is extremely close to the Malawian border and we therefore believe the species occurs in both countries.

Taxonomy. Based on the male terminalia *seyanii* is close to *D. lacertosa* Okada (Table 1).

Etymology. The species is dedicated to Dr. J. H. Seyani, General Secretary 1989–1992 of AETFAT (Association for the Taxonomic Study of the Flora of Tropical Africa) and Director of the National Herbarium and Botanic Gardens of Zomba, Malawi. Dr Seyani organised the Congress and botanical field trips during which the drosophilid collections were made.

Ungrouped species

25) *Drosophila (Drosophila) brachytarsa* Chassagnard & Tsacas, sp. n.

Figs 22–25

Diagnosis. Closely related to *D. (D.) ponera* Tsacas & David, 1983; slightly brownish, pleura brown-striped, fore femur with row of long setae, first tarsomere of fore leg with short, apical, densely spinulate brush, following tarsomeres short.

Male:

Head. Brownish. Frons large, fronto-orbital plate paler, *or1* and *or3* subequal, a row of setulae along eye, upper setulae (*or2*?) arising closer to *or3* and slightly longer. Ocellar triangle dark, postocellar setae short, strong and convergent. Antenna dark, faintly pollinose, arista with 3 dorsal straight and 2 ventral rays plus terminal

fork. Face glossy black in lower half, facial carina narrow with flattened profile, yellow in basal two-thirds, one very strong vibrissa. Clypeus glossy black, palpus yellowish with one subapical seta followed by a second subequal one. Gena broad with anterior half black and posterior half whitish. Eye oblique and dark red.

TABLE 1

Suggested placement of *Drosophila seyanii* in *robusta* species group, based on relative consistency with *D. lacertosa*. Due to lack of material the following characters of Sturtevant (1942) could not be used: posterior malpighian tubes apposed, not with a continuous lumen; 'horns' 2/5 length of puparium. As the character 'with 2 pairs of dorsocentrals' used by Watabe *et al.* (1990) is common to most species of *Drosophila*, it is not considered here. [* = Characters used by Sturtevant (1942)].

Characters of Sturtevant (1942) and Watabe <i>et al.</i> (1990)	<i>robusta</i> species group Watabe <i>et al.</i> (1990)	<i>lacertosa</i> (Myanmar)	<i>seyanii</i> (Malawi)
Body length*	large: 3.5–4.0 mm	3.6 mm	4.3 mm
Colour*	dark brown or black	dark brown	brown
Costal index*	about 4.0	4.3	3.4
Arista*	about 9 bristles	9 bristles	8 bristles
Palpus*	several long bristles besides numerous tiny hairs	3–4 long bristles and numerous tiny hairs	hirsute
Dorsosternals	2 pairs	2 pairs	2 pairs
Acrostichal hairs	6 regular rows	6 regular rows	6 irregular rows
Pre-apicals on tibiae	on all 3 tibiae	on all 3 tibiae	on all 3 tibiae
Apicals on tibiae	on fore and mid tibiae	on fore and mid tibiae	on fore and mid tibiae
Wing colour	hyaline, slightly fuscous	hyaline, slightly fuscous	slightly fuscous
Vein colour	dark brown	dark brown	black
Crossveins	clear	clear	clear
R₂₊₃	straight	straight	straight
R₄₊₅ and M	parallel	parallel	parallel
C₁ bristles	bristles 2, subequal	bristles 2, subequal	bristles 2, subequal
Cercus	fused to epandrium	fused to epandrium	fused to epandrium
Epandrium	pubescent	partly pubescent	partly pubescent
Aedeagus	curved ventrally	curved ventrally	curved ventrally
Anterior paramere	rudimentary or absent	rudimentary	normal
Posterior paramere	absent	absent	absent

Thorax. Scutum not uniformly brownish, slightly paler anteriorly. 6 rows acrostichal setulae, highly differentiated posteriorly. Scutellum and scutum concolorous, subapical scutellar setae convergent, basal scutellar setae almost parallel. Anatergite glossy black. Pleura paler than scutum with a long and broad upper brown stripe with distinctly paler patches, and a short and narrow lower brown

stripe covering upper katepisternum. 3 katepisternal setae, median seta half as long as the two others. Legs slightly darkened, fore femur with a posteroventral row of 5 long setae apically, followed by numerous shorter setae basally. Fore tarsus: first tarsomere long, bearing a shortly spinulate brush and extending antero-apically over second tarsomere, tarsomeres 2–5 short, the second with a faint brush antero-apically, and the third coarsely spinulate. Wing darkened, veins brown, C-index = 3.0. Halter yellowish.

Abdomen. Glossy, yellow with large black bands blending laterally, but with a narrow light band on lateral edges of tergites. Black bands widely interrupted along sagittal line. Last tergite entirely black.

Male terminalia. Epandrium elongate, broader dorsally, ventral epandrial extension bifid with posterior part shorter and bearing 6 strong, long, straight and fan-shaped setae marginally; anterior part longer and narrower with about 10 long and strong setae marginally; posterior edge with dense pollinosity extending slightly dorsally, and 6–8 long setae on each side. Anterior epandrial fragma narrow. Surstylus elongate, with 3 long setae apically, and along inner edge a more or less regular row of 10 or so prenisetae of unequal length shifting regularly from short, strong and more or less ventrally bent basal spines to longer, thinner and straighter apical ones. Cercus elongate, shortly pubescent and irregularly hirsute, basally fused to a process directed ventrally and attached to epandrium there. Hypandrium rectangular, $L/l = 1.5$, posterior edge of novasternum indented medially, paramedial setae strong and short, arising distantly from one another; posterodorsal parts extending backwards around aedeagus. Anterior parameres short, narrow, with 3 long setae each. Aedeagus long and broad, attached to epandrium along a small basal line only. Distiphallus with highly complex structure, trifid, its ventral part disk-like, the two other dorsal parts, which are almost cylindrical.

Female. Unknown.

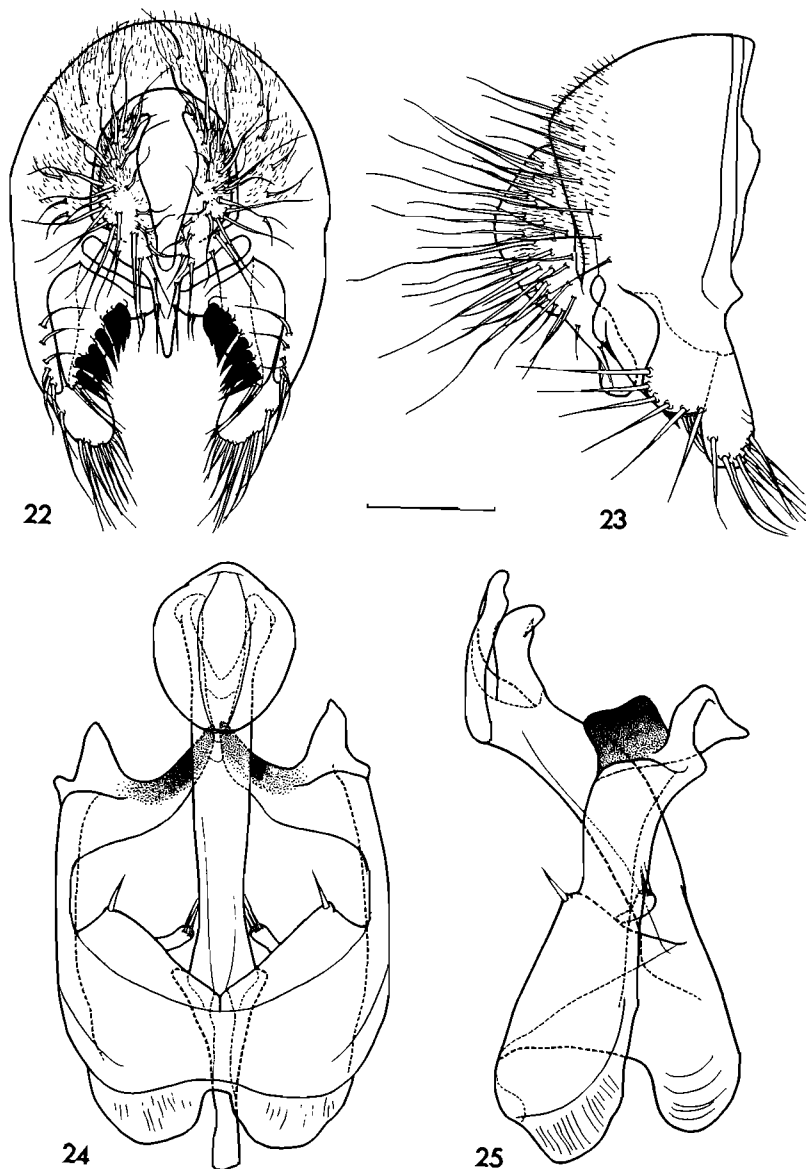
Length (in mm): Male. Body 3.0; wing 2.8.

Material examined: Holotype ♂: MALAŴI: Lilongwe, 20.iv.1991 (Lachaise) (MNHNP). Paratypes: KENYA: 1♂, Mt Elgon, 2880 m, clearing in *Podocarpus* forest, on fallen fruits 'berries' of *Rhamnus prinoides* (Rhamnaceae), ix.1984 (Lachaise, Cariou, Ashburner) (MNHNP); TANZANIA (Tanganyika): 1♂, Mahali (Makari) Peninsula, Kungwe Camp, Forest clearing, 6000 feet (1829 m), 10.xi.1995 (2nd Oxford U. Exped.), B.M. 1960-279 (NM); ZAÏRE (ex CONGO BELGE): 1♂, PNU (Upemba National Park), Lusinga riv., near Mukana, 1.vi.1945 (de Witte); 1♂, *ide*, but Komituno riv. (tributary of Lusinga riv.), 10.vii.1945 (de Witte) (MRAC).

Distribution. Malaŵi, Zaïre, Kenya, Tanzania.

Taxonomy. *Drosophila brachytarsa* belongs to the subgenus *Drosophila s. str.*; it is closely related to *D. ponera* Tsacas & David, which was described from Réunion, but has since been reported from Cameroun (new record).

Etymology. From Greek βραχυς = short and ταρσος = tarsus. Refers to the short fore tarsus.



Figs 22–25. *Drosophila (Drosophila) brachytarsa* Chassagnard & Tsacas sp. n. 22. Epandrium and associated structures, caudal view. 23. *idem*, lateral view. 24. Hypandrium and associated structures, ventral view. 25. *idem*, lateral view. Scale: 0.1 mm.

26) *Drosophila (Drosophila) adamsi* Wheeler, 1959

Drosophila (D.) quadrimaculata Adams, 1905 [preocc.] is a synonym.

Material examined: MALAWI: 1♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Zimbabwe, Ethiopia, Nigeria, Cameroun, Central African Republic, Uganda, Kenya, South Africa, Malawi (new record).

27) *Drosophila (Drosophila) adamsi* Chassagnard & Tsacas, sp. n.

Figs 26–32

Diagnosis. Very closely related to *D. adamsi* Wheeler, the distinctive character being the male terminalia.

Male:

Head. Frons markedly narrowed anteriorly, double brown bands along broad fronto-orbital plate covered with faint silvery pollinosity, golden brown in the middle. Ocellar triangle blackened, ocellus golden brown. Orbital setae: *or1* and *or3* subequal, *or2* short, slender and arising noticeably closer to *or1*. Postocellar setae long and convergent. Face dull white, facial carina well marked, narrow with sharp edge; anterior border brown-banded. Clypeus small, brown. Palpus yellowish with 2 subapical setae and a third more distant one. Antenna: pedicel blackened-brown, flagellum concolorous paler on inner basal side, arista with 5 long dorsal rays, and 2 ventral rays arising distantly from one another, plus terminal fork. Strong vibrissa followed by 2 other more slender setae. Gena narrow, slightly brownish. Eye as in *D. adamsi*.

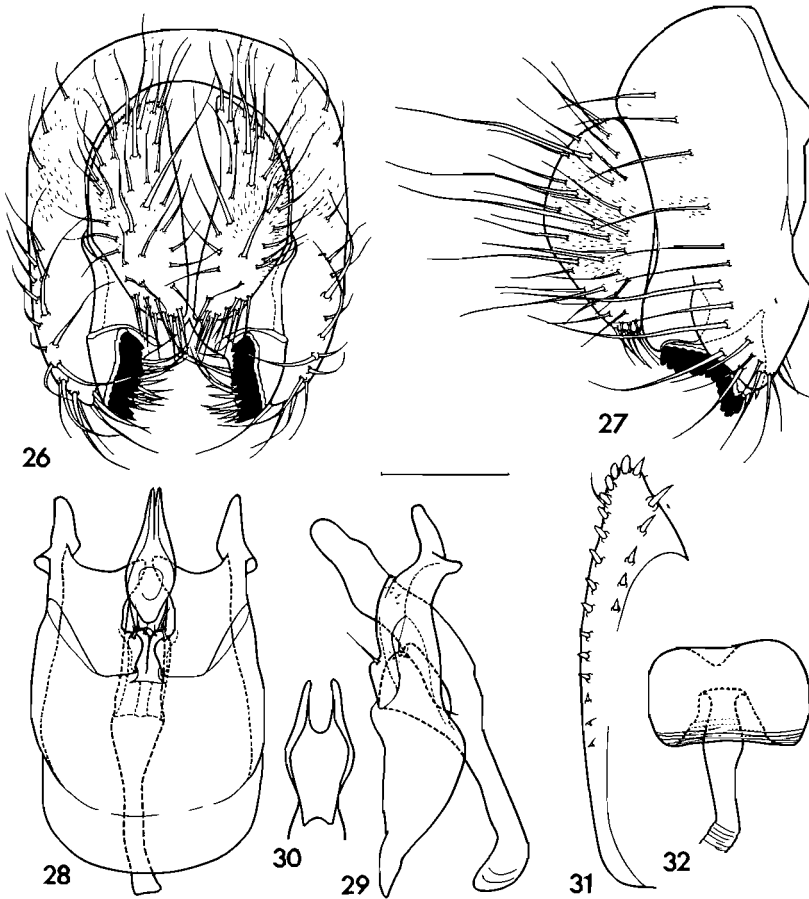
Thorax. Scutum brownish-yellow with 6 longitudinal bands, the lateral ones more diffuse and the 2 median ones slightly broader posteriorly; mid band pale and narrower than others. 6 rows of acrostichal setulae. Chaetotaxy as in *adamsi*. Scutellum brownish, elongate, tapering apically and slightly paler laterally. Pleura pale yellow with 3 brown bands, the upper ending at wing base, the mid one as long as pleural length, the lower fringing upper border of katepisternum. 3 katepisternal setae, the posterior strong and long, the 2 others subequal. Legs as in *adamsi*. Wing as in *adamsi* with similar brown patches but narrow and darker. Halter with stem brown anteriorly and capitulum brownish.

Abdomen. Yellow with a broad brown band on every tergite, brown laterally; last tergite glossy black with pale patches antero-laterally.

Female: Similar to male.

Male terminalia. Epandrium brown except lower part whitish, broad, bare except postero-superior fourth shortly pollinose, a row of 12 long setae arising close to posterior border and ventral epandrial expansion with 12 unequal generally shorter setae. Epandrial fragma relatively short and narrow. Surstylus elongate, bearing 15 strong prenisetae arranged in a long row which generally appears sinuous yet sometimes straight or merely bent; inside the row of prenisetae are also 12 short setae the 2 or 3 apical markedly longer. Cercus densely covered with short pubescence except on lower part which bears apically a cluster of relatively short and straight setae, cercus otherwise covered with very unequal setae. Hypandrium orthogonal, bare, with deep narrow groove posteromedially, submedian setae short and arising close to one another; anterior paramere narrow, straight, bearing 3 setulae. Aedeagus slightly incurved ventrally, distiphallus leaf-like folded along a sagittal dorsal line, and with deep apical indentation alternatively narrow or large according to individuals (Figs 28 & 30). [This difference is intriguing and may correspond to two different stages of the erection process, or be an artefact due to preparation treatment]. In lateral view distiphallus appears rounded.

Female terminalia. Ovipositor tapering with row of 16 teeth of which the 4 apical ones are the longest and most closely set; the following teeth decrease gradually in size and are progressively distantly set. Dorsally is an oblique row of 5 teeth, the apical one being the longest. Spermathecal width larger than height.



Figs 26–32. *Drosophila (Drosophila) adamisa* Chassagnard & Tsacas sp. n. 26. Epandrium and associated structures, caudal view. 27. *idem*, lateral view. 28. Hypandrium and associated structures, ventral view. 29. *idem*, lateral view. 30. Distiphallus, ventral view. 31. Ovipositor. 32. Spermatheca. Scale: 0.1 mm.

Length (in mm): Male. Body 3.9; wing 3.8. *Female.* Body 3.9; wing 3.9.

Material examined: Holotype ♂, MALAWI: Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP). Paratypes, 1♂1♀, *idem* (NM); 2♂3♀, KENYA: Mount Elgon 1, submontane forest, 2290 m, on fruits of *Diospyros abyssinica* (Hiern) F. White (Ebenaceae), 2.ix.1984 (Lachaise, Cariou, Ashburner) (MNHNP). Other material: 1♂, MALAWI: Ntchisi Forest Reserve, 1334Ac, Montane forest & woodland, 1500 m, 3–4.xii.1980 (Londt & Stuckenberg) (NM).

Distribution. Malaŵi, Kenya.

Etymology. The name is derived from *adamsi*, to which this species is most closely related.

The two following species (known from females only) are not described. They probably belong to the *robusta* species group, yet the lack of males makes definitive assignment questionable.

28) *Drosophila (Drosophila)* sp. A

Material examined: MALAŴI-ZAMBIA: 2♀, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP).

These two females are very close to *D. (D.) seyanii*, differing by brownish colouration, the abdomen black except the two last tergites entirely pale, and spermatheca globulous.

29) *Drosophila (Drosophila)* sp. B

Material examined: MALAŴI-ZAMBIA: 2♀, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP).

These two females are also very close to *D. seyanii* and *Drosophila (D.)* sp. A, the distinctive character being the glossy black abdomen, contrasting with the rusty brown thorax.

Subgenus *Sophophora* Sturtevant, 1939

This subgenus is well represented in Malaŵi, and more generally in the Afrotropical Region, including especially the *melanogaster* species group and endemic species groups like the *dentissima* and *fima* species groups.

dentissima group Tsacas, 1980

This group presently comprises 16 montane species, with two species in Malaŵi.

30) *Drosophila (Sophophora) dentissima* Bock & Wheeler, 1972

Material examined: MALAŴI: 1♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. South Africa, Malaŵi (new record). This species was hitherto known only from South Africa (Tsacas 1990); its presence in Malaŵi extends significantly its geographical range north-westwards.

Taxonomy. This species can be assigned to the *dentissima* species complex (Tsacas 1980b).

31) *Drosophila (Sophophora) kivuensis* Tsacas, 1980

Material examined: MALAŴI-ZAMBIA: 2♂, Nyika Plateau, Chowo forest, 2120m, 14.iv.1991 (Lachaise) (MNHNP).

Distribution. Uganda, Zaïre, Malaŵi (new record), Zambia (new record). These new localities extend significantly the geographical range of the species southwards.

Taxonomy. This species can be assigned to the *dentissima* species complex.

fima group Burla, 1954

This afrotropical species group is presently comprised of 17 fig-breeding species (most strictly fig dependent). It is represented in Malaŵi by 3 species, 2 of which are new. Both new species – *dimitroides* and *neomitra* – belong to the *dyula* species complex characterised by combs on the first two tarsomeres of the fore legs.

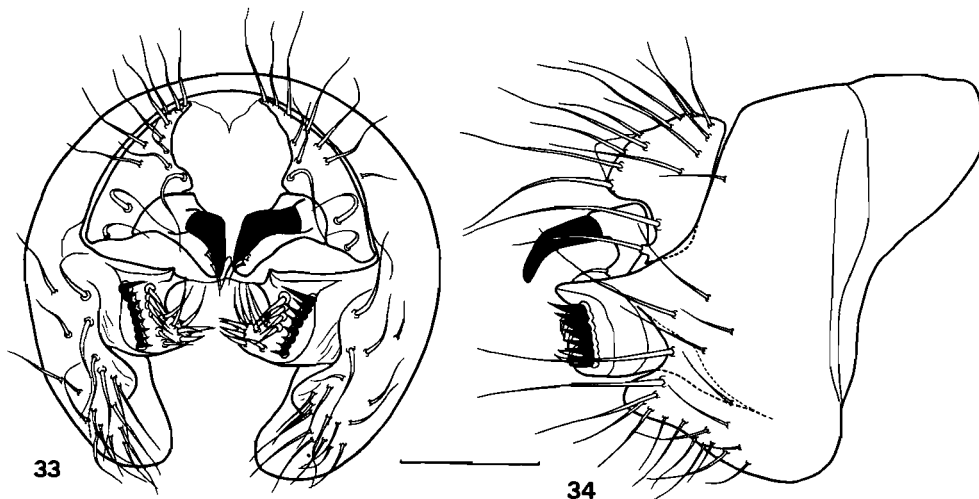
32) *Drosophila* (*Sophophora*) *dimitroides* Chassagnard & Tsacas, sp. n.

Figs 33–34, 35–36

Diagnosis. Close to *D. dimitra* Tsacas based on male terminalia, but differing unambiguously from this species by the brownish colouration of its pleura. It is also closely related to *sycovora* and *neomitra*, considering other phenotypic characters used in the key given below.

Male/Female:

Head. Frons brownish, fainter on anterior border, fronto-orbital plate glossy brown, becoming wider ventrally, *or1* and *or3* arising close to each other, subequal, *or2* filiform and short. Ocellar triangle brown, ocellar setae long and parallel. Antenna brown, arista with 5 dorsal and 2 ventral rays plus terminal fork. 2 vibrissae the second at least two-thirds of the first. Gena linear.



Figs 33–34. *Drosophila* (*Sophophora*) *dimitroides* Chassagnard & Tsacas sp. n. 33. Epandrium and associated structures, caudal view. 34. *idem*, lateral view. Scale: 0.1 mm.

Thorax. Glossy; scutum reddish-brown, darker posteriorly and laterally. 6 rows of acrostichal setulae, posterior dorsocentral setae long. Pleura brown. Scutellum brown. Legs pale, fore femur slightly darkened, fore tarsus: first and second tarsomeres with short transversal sex comb comprised of 2–3 teeth apically, second tarsomere largely overlapping the third. Wing darkened.

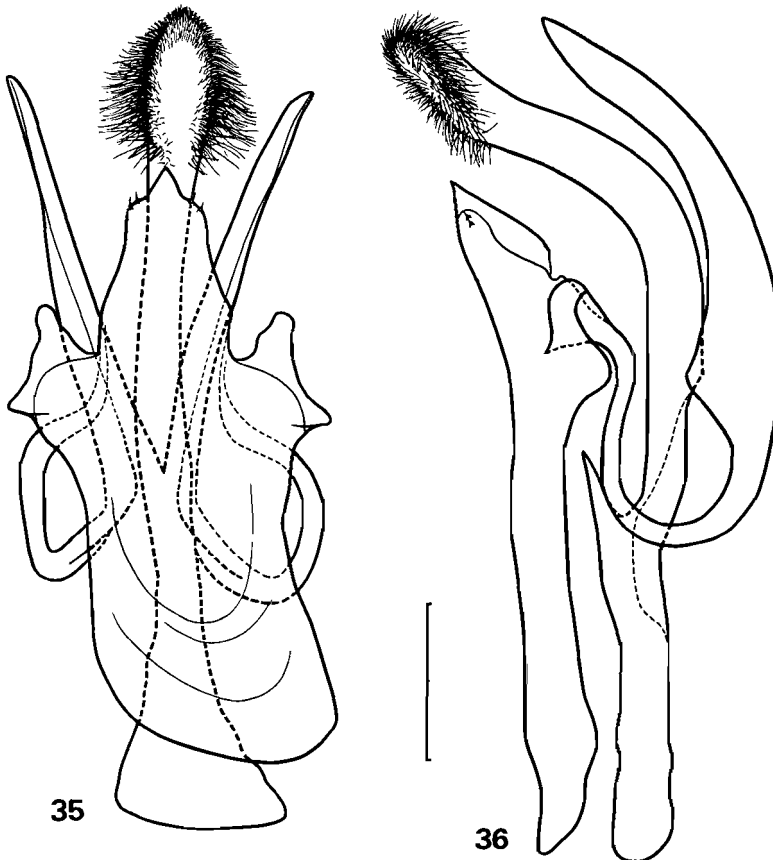
Abdomen. Black.

Male terminalia. Epandrium similar to *D. dimitra* Tsacas, differing by: posterior

edge of epandrium making a lobe below surstylus, 1 isolated seta on each side of dorsal half of epandrium posteriorly, numerous setae on ventral half, the 3 longest at level of surstylus. Cercus largely scalloped posteroventrally, with *ca.* 15 long setae, the longer on posteroventral edge. Secondary clasper crescent-shaped, upper tip tapering in a stout sickle-shaped process ventrally bent, lower tip with 2 relatively short setae. Surstylus with 8 strong teeth, the uppermost significantly larger, in a straight row along external margin, 6 large other prenisetae more internally, the 2 lower straight and the 4 upper bent, and a cluster of 6 slender setae at extremity. Hypandrium similar albeit larger than that of *D. dimitra*, differing mostly by the posterior end tapering in the middle and becoming inflexed on both sides, each with 2 short setae arising close to each other. Distiphallus more elongate and with longer hairs than in *D. dimitra*; anterior paramere simpler and more sharply pointed.

Female. Unknown.

Length (in mm): Male. Body 1.8; wing 1.7.



Figs 35–36. *Drosophila (Sophophora) dimitroides* Chassagnard & Tsacas sp. n. 35. Hypandrium and associated structures, ventral view. 36. *idem*, lateral view. Scale: 0.1 mm.

Material examined: MALAŴI: Holotype ♂ (unique), Zomba, Chancellor College, 790 m, iv.1991, sweeping above fallen figs of *Ficus thonningii* (Lachaise) (MNHNP).
Distribution. Malaŵi.

Taxonomy. *D. dimitroides* sp. n. and *D. neomitra* sp. n. described below, belong to the so-called *modified fore tarsus male* 'unit' within the *fima* species group, and fit in the key published in Tsacas & Lachaise (1981) as follows:

- 3 Fore femur with numerous long setae, sexual comb double.....**dyula** Tsacas
- Fore femur without numerous long setae, sexual comb simple3a
- 3a Frons brown concolorous with fronto-orbital plate.....**syconvora** Tsacas
- Frons yellowish-brown, significantly paler than fronto-orbital plate.....3b
- 3b Fore femur and wings darkened.....**dimitroides** Chassagnard & Tsacas, sp. n.
- Fore femur and wings pale**neomitra** Chassagnard & Tsacas, sp. n.

Etymology. The name indicates its close relatedness with *D. dimitra*.

33) *Drosophila (Sophophora) fima* Burla, 1954

Material examined: MALAŴI: 67♂♀, Zomba Plateau, Chancellor College, 790 m, 5.iv.1991, above fallen figs of *Ficus thonningii*; 9♂♀, *idem* but above fallen figs of *Ficus sycomorus*; 3♂♀, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.91 (Lachaise) (MNHNP).

Distribution. Ivory Coast, Nigeria, Cameroun, Central African Republic, Gabon, Congo, Burundi, Tanzania, South Africa, Malaŵi (new record).

Taxonomy. The species belongs to the *non-modified fore tarsus male* 'unit' within the *fima* group (Tsacas & Lachaise 1981).

34) *Drosophila (Sophophora) neomitra* Chassagnard & Tsacas, sp. n.

Figs 37–40

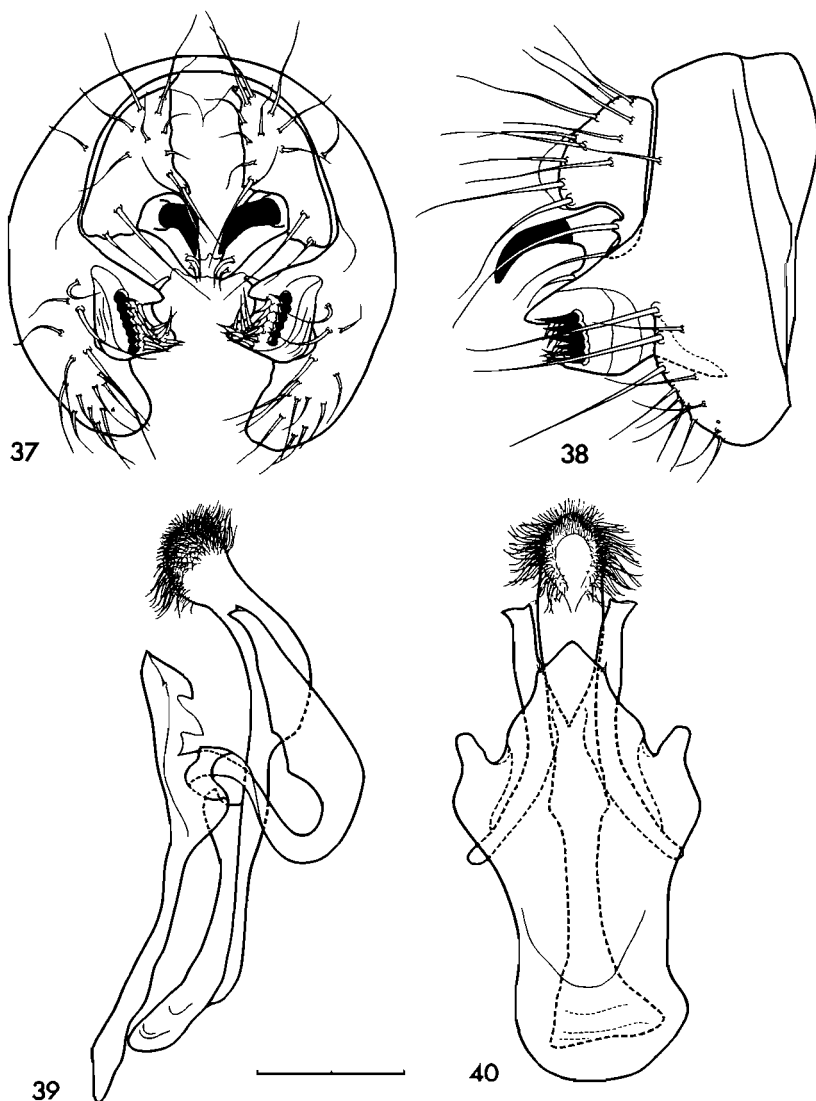
Diagnosis. Close to *D. dimitroides*, differing in the male terminalia and characters given in the above key.

Male terminalia. Anterior epandrial fragma broad, extending up to ventral extremity of epandrium, no lobe below surstylus, 1 isolated seta on each side of dorsal half of epandrium posteriorly, 3 long setae at level of surstylus, followed by 10 shorter setae more ventrally. Cercus as in *D. dimitroides*, with 12 long setae. Secondary clasper as in *D. dimitroides*, yet with longer stout sickle-shaped process less markedly bent. Surstylus with 6–7 strong teeth in straight row along external margin, 6 large other prenisetae more internally, and a cluster of 5 prenisetae irregularly disposed at extremity. Hypandrium as in *D. dimitroides*, slightly less tapered and more incurved ventrally. Parameres long, markedly bent, inflated dorsally before tip which ends truncated with 2 points. Aedeagus long, smoothly bent and swollen medially; distiphallus globose in lateral view, densely hirsute apically and around gonopore.

Female: Unknown.

Length (in mm). *Male.* Body 2.0; wing 1.9.

Material examined: MALAŴI: Holotype ♂ (unique), Zomba Plateau, Chancellor



Figs 37–40. *Drosophila (Sophophora) neomitra* Chassagnard & Tsacas sp. n. 37. Epandrium and associated structures, caudal view. 38. *idem*, lateral view. 39. Hypandrium and associated structures, lateral view. 40. *idem*, ventral view. Scale: 0.1 mm.

College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 5.iv.1991 (Lachaise) (MNHNP).

Distribution. Malawi.

Taxonomy. See *D. dimitroides*.

Etymology. Name composed of *neo* and the two last syllables of *dimitra*, indicating thereby its relatedness with this latter species.

melanogaster group Sturtevant, 1942*melanogaster* subgroup

This strictly afrotropical species subgroup, the two cosmopolitan species excepted, has long been paid substantial attention by population geneticists and evolutionary biologists.

35) *Drosophila (Sophophora) melanogaster* Meigen, 1830

Material examined: MALAWI: 1♂1♀, Zomba plateau, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 5.iv.1991; 1♂, Lilongwe, 1000 m, 20.iv.1991; 44♂26♀, Kasungu National Park, 28.iii.1991; 2♂, Luwawa Forest Reserve, Luwawa Pond, *Pinus* forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Cosmopolitan.

Further material examined: MALAWI: 26♂ caught alive in Kasungu National Park (19.iv.1991) were used in experimental crosses; 2♀ from Zomba, 12♀ from Lilongwe, 20.iv.1991, 50♀ from Kasungu, 18–19.iv.1991, 1♀ from Luwawa, 12.iv.1991, were caught alive (Lachaise) and used as foundresses of isofemale lines used for analysis of between-population molecular variation of alcohol dehydrogenase restriction enzymes (Bénassi & Veuille 1995).

36) *Drosophila (Sophophora) simulans* Sturtevant, 1919

Material examined: MALAWI: 15♂6♀, Zomba Plateau, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 3–11.iv.1991; 1♂22♀, Lilongwe, 1000 m, 20.iv.1991; 3♀, Kasungu National Park, 28.iii.1991; 2♂, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991; 8♂, Nyika Plateau, Chilinda, 2250 m, 15–16.iv.1991 (Lachaise) (MNHNP). Wild-caught females were used to found 6 and 5 isofemale lines from Zomba and Nyika-Chilinda respectively, and 11 and 6 multifemale lines from Lilongwe and Kasungu respectively.

Distribution. Cosmopolitan.

37) *Drosophila (Sophophora) yakuba* Burla, 1954

Material examined: MALAWI: Several dozen ♂♀, Zomba Plateau, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 3–11.iv.1991; 1♀, Lake Malaŵi National Park, Cape Maclear, 30.iii.1991; 3♀, Kasungu National Park, 28.iii.1991 (Lachaise) (MNHNP).

Distribution. Ivory Coast, Senegal, Gambia, Nigeria, Cameroun, Gabon, Congo, Zaïre, Uganda, Kenya, Burundi, Tanzania, Zimbabwe, South Africa, Madagascar, Bioko (Fernando Po), Malaŵi (new record).

Discussion. The two cosmopolitan sister species (*melanogaster* and *simulans*) excepted, *D. yakuba* is the most widespread species of the *melanogaster* subgroup within the Afrotropical Region, uniquely extending its geographical range to Madagascar and Bioko.

montium subgroup Hsu, 194938) *Drosophila (Sophophora) burlai* Tsacas & Lachaise, 1974

Material examined: MALAWI: 3♂, Zomba Plateau, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, iv.1991; 1♂, Lake Malaŵi National Park, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 2♂, Luwawa Forest Reserve, Luwawa Pond, *Pinus* forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP). A total of 17 wild-caught ♀ ♀ from Kasungu National Park, 1040 m, 18.iv.1991, were used as foundresses of the same number of isofemale lines.

Distribution. Ivory Coast, Gambia, Senegal, Nigeria, Cameroun, Central African Republic, Gabon, Congo, Zaïre, Uganda, Tanzania, Malaŵi (new record).

39) *Drosophila (Sophophora) greeni* Bock & Wheeler, 1972

Material examined: MALAWI: 5♂, Zomba Plateau, Chancellor College, 790 m, swept above fallen figs of *Ficus thonningii*, 8.iv.1991; 9♂, Lake Malaŵi National Park, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 2♂, Kasungu National Park, 28.iii.1991 (Lachaise) (MNHNP). A total of 18 wild-caught females from Kasungu were used as foundresses of the same number of isofemale lines.

Distribution. Zimbabwe, Senegal, Gambia, Guinea, Ivory Coast, Benin, Nigeria, Cameroun, Central African Republic, Gabon, Congo, Malaŵi (new record).

40) *Drosophila (Sophophora) ifestia* Tsacas, 1984

Material examined: MALAWI: 1♂, Nyika Plateau, Chilinda, 2250 m, 15–16.iv.1991. MALAWI-ZAMBIA: 2♂, Nyika Plateau, Chowo Forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP).

Distribution. Zaïre (Ruwenzori, Kivu); Uganda, Kenya, Burundi, Rwanda, Malaŵi (new record), Zambia (new record).

bakoue complex

This complex is composed of the following species: *bakoue* Tsacas & Lachaise, 1974; *greeni* Bock & Wheeler, 1972; *malagassya* Tsacas & Rafael, 1982; *seguyi* Smart, 1945; *tsacasi* Bock & Wheeler, 1972; *vulcana* Graber, 1957. In the sample from Malaŵi we recognized four unknown species, including 2 new species described here and 2 presumably new but which cannot be satisfactorily described. Although a first study was devoted to this difficult complex of closely related species (Rafael 1984), many taxonomic points have remained unclear.

41) *Drosophila (Sophophora) bakoue* Tsacas & Lachaise, 1974

Material examined: MALAWI: 2♂, Zomba Plateau, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 5.iv.1991; 23♂♀, Lake Malaŵi National Park, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 15♂♀, Kasungu National Park, iii.1991, *ex* isofemale line 296.3 Gif-stock (Lachaise) (MNHNP).

Distribution. Ivory Coast, Benin, Nigeria, Cameroun, Gabon, Congo, Malaŵi (new record).

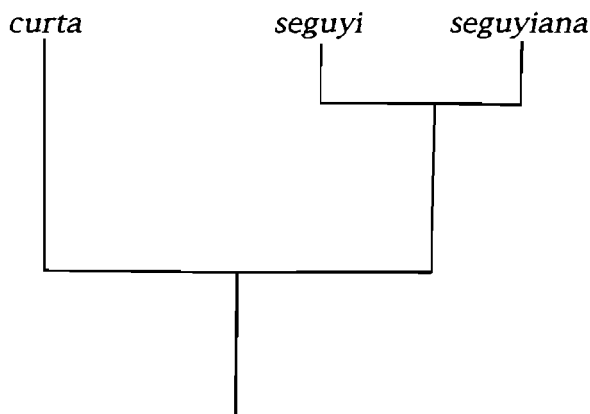


Fig. 41. Cladogram of the species of the *Drosophila (Sophophora) seguyi* complex.

42) *Drosophila (Sophophora) seguyi* Smart, 1945

Material examined: MALAWI: 4♂2♀, Zomba Plateau, Chancellor College, 790 m, swept above fallen figs of *Ficus thonningii*, 5.iv.1991; 1♂, Lake Malaŵi National Park, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 1♂, Kasungu National Park, iv.1991 (Lachaise) (MNHNP).

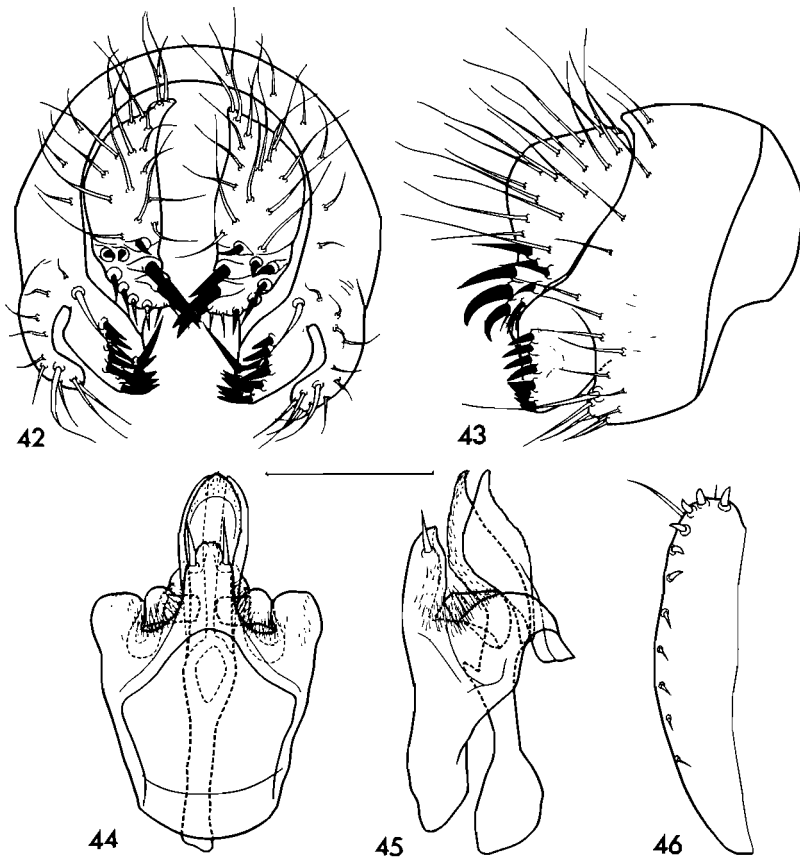
Distribution. Kenya, Tanzania, Malaŵi (new record).

TABLE 2
Distinctive characters within *Drosophila seguyi* species complex.

Character	<i>D. seguyi</i>	<i>D. seguyiana</i>	<i>D. curta</i>
1. Surstylus	9–10 long setae	10 long setae	12 short setae
2. Aedeagus relative to posterior paramere	longer	longer	equal
3. Aedeagus width	narrow	narrow	wide
4. Aedeagus shape	straight	straight	incurved
5. Medial extension of novasternum (ventral view)	tapering, non-serrated	tapering, non-serrated	truncated and serrated
6. Medial extension of novasternum (lateral view)	finger-like	finger-like	beak-shaped
7. Anterior paramere position	vertical	oblique	horizontal
8. Anterior paramere shape	lobate	non-lobate	lobate
9. Secondary clasper	3 setae	5 setae	3 setae

Taxonomy. *D. seguyi*, *D. curta* sp. n. and *D. seguyiana* sp. n. are a cluster of very closely related species to which *Drosophila* sp. D could be added. The reason why the latter species is excluded is explained below. A few conclusions on species relatedness between the three former species can be derived (Fig. 41) from the analysis of 9 traits of male terminalia summarised in Table 2. This clearly shows that

D. curta, with seven characters not found in the other species (that is alternative characters concerning traits 1–7), two in common with *seguyi* (8,9) and none shared with *seguyiana*, is the most distantly related species. The two others have six characters in common (1–6) and are separated by three (7–9) characters uniquely found in *seguyi* and *seguyiana* respectively. These three species can be seen as a taxonomic unit (the *seguyi* species cluster) which together with *Drosophila* sp. D is an entity within the *bakoue* species complex.



Figs 42–46. *Drosophila (Sophophora) curta* Chassagnard & Tsacas sp. n. 42. Epandrium and associated structures, caudal view. 43. *idem*, lateral view. 44. Hypandrium and associated structures, ventral view. 45. *idem*, lateral view. 46. Ovipositor. Scale: 0.1 mm.

43) *Drosophila (Sophophora) curta* Chassagnard & Tsacas, sp. n.

Figs 42–46, 51–54

Diagnosis. Close to *D. seguyi*, differing by the black tergites 5 and 6 and the truncated median prominence of the posterior border of the epandrium.

Male/Female:

Head. Rusty brown, anterior band lighter. Fronto-orbital plate dark and greyish

pollinose, *or*1 shorter than *or*3, *or*2 short and fine, arising about half distance from the 2 others. Postocellar setae convergent. Antenna: pedicel concolorous with anterior frontal band, flagellum brown, arista with 5 dorsal and 3 ventral rays plus terminal fork. Face glossy brown, facial carina hardly prominent with whitish edge. Palpus rusty yellow with a strong subapical seta.

Thorax. Scutum rusty brown. 6 rows of acrostichal setulae. 2 pairs dorsocentral setae, posterior one invariably bent outwards. Scutellum darker than scutum, basal scutellar setae parallel, apical scutellar setae strongly crossed. Pleura concolorous with scutum or slightly darker. Legs pale, fore tarsus combs like that of *seguyiana* yet somewhat longer (19–20 teeth against 13–15 in *seguyiana*). Wing darkened, veins brown. Halter concolorous with pleura.

Abdomen. Black, tergites 2–4 with yellowish band anteriorly which may sometimes not reach lateral edge. Tergites 5 and 6 entirely black.

Male terminalia. Epandrium large, brown without faint pubescence, epandrial fragma extending up to upper two-thirds of its anterior edge; it bears, on each side near its posterior edge about 12 moderately sized setae followed by a very long seta, on posterior end of ventral epandrial lobe are also about 12 similar moderately sized setae. Cercus prominent, bearing long setae, on their ventral extension ('secondary clasper') is a series of 3 strong setae: the upper one almost straight, the mid one bent ventrally, the lower one shorter and still more curved; at edge of secondary clasper and cercus are 3 less robust setae, followed latero-ventrally by a series of 6–7 marginal teeth the size of which decreases gradually. Surstylus slightly elongated dorsoventrally with 12 strong prensisetae, the most internal and longest one pointing upwards, the 5 most lateral ones making a vertical row, the remaining setae in a cluster at posteroventral end of surstylus. Hypandrium slightly longer than large, with a medial extension of novasternum truncated and serrated posteriorly, flanked by 2 paramedian setae thick and far apart; anterior parameres long, transverse, larger in their lateral one-third and bearing 3 close-set sensillae mediodorsally; posterior parameres as long as aedeagus, S-shaped, swollen medially in lateral view, tapering and incurved medioposteriorly, slightly serrated dorsally. Aedeagus very alike posterior parameres (S-shaped), swollen medially in lateral view, tapering and incurved medioposteriorly, distiphallus slightly pointed in ventral view and faintly pubescent. Aedeagal apodeme broadened laterally.

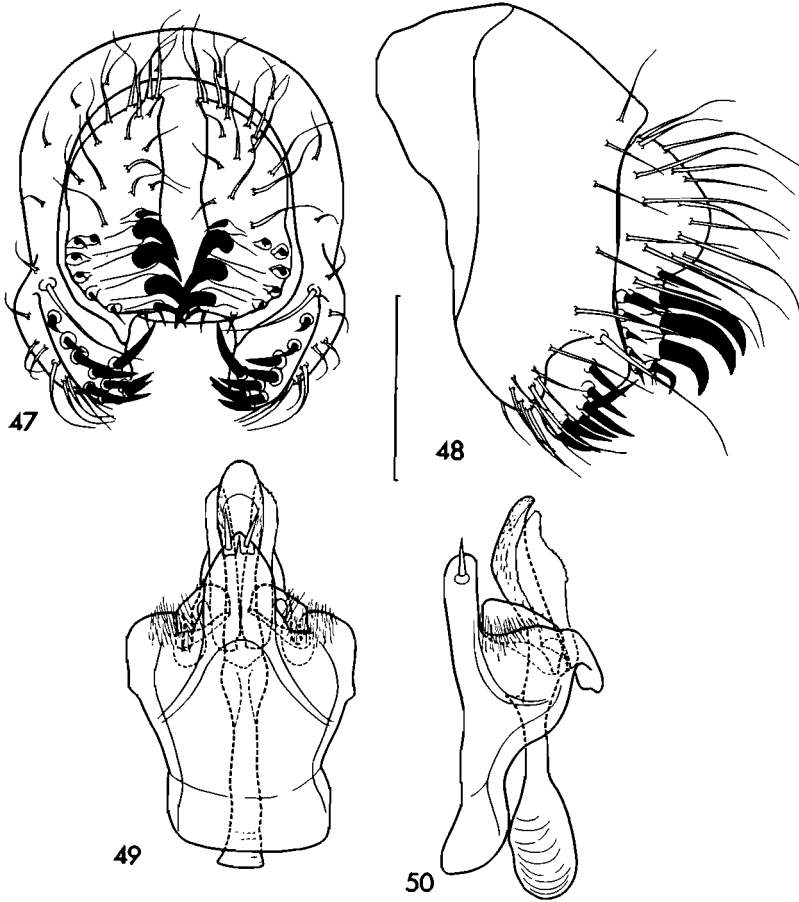
Female terminalia. Ovipositor narrow, elongate, with 11 short marginal setae of which the first 6 are significantly stronger, a setula between first and second teeth, and a long seta between third and fourth teeth.

Length (in mm): *Male.* Body 2.6; wing 2.1. *Female.* Body 2.8; wing 2.3.

Material examined: MALAWI: Holotype ♂, Cape Maclear, dry ravine, *Brachystegia* woodland, *ex* strain no 296.1 (isofemale line), 30.iii.1991 (Lachaise) (MNHN). *Paratypes*, 56♂♀, *idem* (MNHN); 2♂2♀, *idem* but (NM); 4♂2♀, *idem* but *ex* strain no 296.2 (isofemale line); 9♂♀, *idem* but *ex* non numbered strain.

Distribution. Malawi.

Etymology. From Latin, *curtus* = short. Refers to the distinctive medial extension of the novasternum which is truncated posteriorly.



Figs 47–50. *Drosophila (Sophophora) seguyiana* Chassagnard & Tsacas sp. n. 47. Epandrium and associated structures, caudal view. 48. *idem*, lateral view. 49. Hypandrium and associated structures, ventral view. 50. *idem*, lateral view. Scale: 0.1 mm.

44) *Drosophila (Sophophora) seguyiana* Chassagnard & Tsacas, sp. n.

Figs 47–50, 55–58

Diagnosis. Concolorous with *D. seguyi*, especially with respect to similarly coloured tergites: T2–T5 with a large posterior brown or black band, and T6 black; male terminalia strongly distinct: median prominence of posterior border of hypandrium tapering, as in *D. seguyiana*, but with paramedian setae arising close to each other, and aedeagus longer than posterior parameres.

Male:

Head. Frons brown with large dark yellow band anteriorly, extending medially toward ocellar triangle in some specimens. Fronto-orbital plate glossy; *or*1 and *or*3 subequal, *or*2 half length and arising closer to *or*1. Face glossy greyish-white, facial carina narrow and hardly prominent. Antenna: pedicel concolorous with anterior

frontal band, flagellum brownish, darker dorsally, arista with 4–5 dorsal and 2–3 ventral rays plus terminal fork.

Thorax. Scutum rusty brown, darker posteriorly, 6 rows of acrostichal setulae. Scutellum concolorous with posterior end of scutum. Pleura slightly paler than scutum. Legs brownish yellow, mid and hind coxa paler; first tarsomere of fore leg with long tarsal comb composed of 17 teeth, the proximal ones close-set, the others longer and further apart, the last two arising close together; second tarsomere of fore leg shorter, with tarsal comb composed of 16 close-set teeth. Wing darkened, veins brown, C-index = 2.6. Halter with yellow stem and rusty brown capitulum.

Abdomen. Rusty brown: T2–T5 with large band posteriorly, brown from T2–T4 and black on T5, T6 glossy black.

Male terminalia. Epandrium, cercus, surstylus and medial extension of posterior edge of hypandrium black. Epandrium wide, without pubescence, epandrial fragma large, in caudal view ventral epandrial lobes stand out making a swelling in lower half of epandrium; it bears, on each side, near its posterior edge, 5–6 relatively short setae followed by a sixth very long seta ventrally; on posterior end of ventral epandrial lobe are also about 12 unequally-sized setae. Cercus bulging, bearing long setae, on their ventral extension ('secondary clasper') is a series of 5 strong setae, the medial 3 very stout and strongly bent ventrally, the upper one fine, short and slender, the lower one similar to this but strongly bent ventrally. Also on cercus area is laterally a series of 5–6 compact small setae of which size decreases from upper to lower, it is followed by 2 short setae medially. Surstylus with 10 strong subequally-sized prenisetae, except innermost which is significantly longer. Hypandrium slightly longer than wide, with medial extension of novasternum long, large and tapered posteriorly, flanked by 2 short paramedian setae, thick and close-set; on each side of medial extension of novasternum is a pubescent patch; anterior parameres wide, slanting, and bearing 3 long sensillae mediodorsally; posterior parameres elongate, slightly shorter than aedeagus, ending straight, not incurved internally, edges slightly serrated. Aedeagus S-shaped and tapered laterally, large and blunt dorsally, pubescent ventrally. Aedeagal apodeme base broadened laterally.

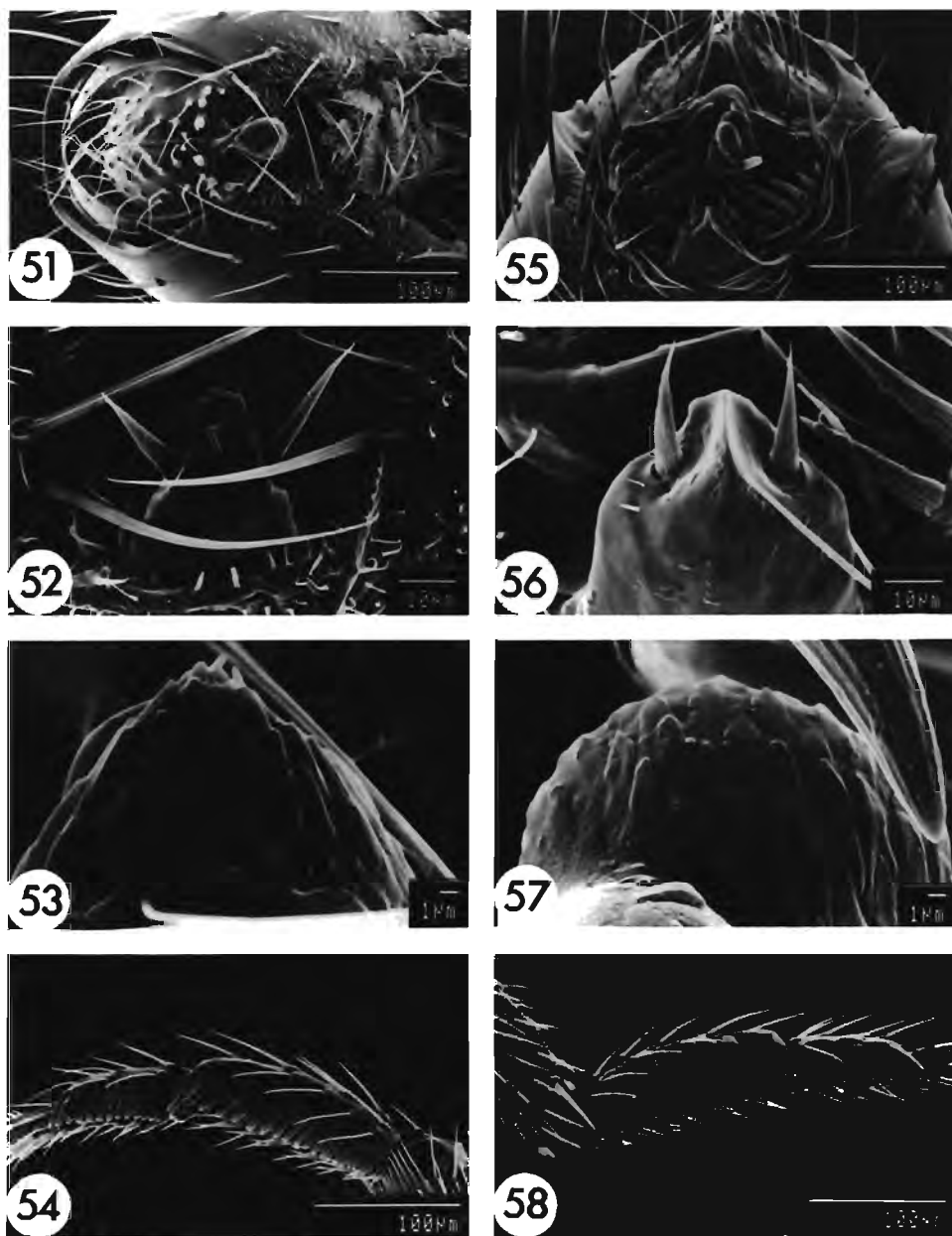
Female: Unknown. Although a series of wild-caught females presumably belong to this species, they could not be unequivocally associated due to the presence of females of *D. bakoue*, *D. burlai*, *D. curta* sp. n., *D. greeni*, *D. seguyi* and *D. sp. C*, at the same localities.

Length (in mm): Male. Body 2.4; wing 2.2.

Material examined: MALAWI: Holotype ♂, Zomba Plateau, 790 m, sweeping above fallen figs of *Ficus sycomorus*, 5.iv.1991; Paratypes, 4♂, *idem* (MNHNP); 2♂, *idem* but (NM); 8♂, *idem* but above fallen figs of *Ficus thonningii*; 9♂, Viphyia Plateau, Luwawa Pond, *Pinus* forest reserve, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Malawi.

Etymology. Dedicated in honour of Prof. Eugène Seguy's memory and indicating the affinity of the new species with *D. seguyi*.



Figs 51–58. Comparative views of the closely related species *Drosophila curta* Chassagnard & Tsacas sp. n. and *D. seguyiana* Chassagnard & Tsacas sp. n. 51–54. *D. curta*. 51. Male terminalia, posteroventral view. 52. Medial extension of hypandrium. 53. Apical end of distiphallus. 54. Fore tarsi and sexual combs. 55–58. *D. seguyiana*. 55. Male terminalia, ventral view. 56. Medial extension of hypandrium. 57. Apical end of distiphallus. 58. Fore tarsi and sexual combs.

45) *Drosophila (Sophophora)* sp. C

Material examined: MALAWI: 4♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Although the male terminalia are close to those of *D. seguyi*, this species exhibits an abdominal colouration distinct from *seguyi* (that is T2–T4 diffuse brown, T5 and T6 pale like terminalia). It is therefore probably a new species but we do not describe it here since it cannot be reliably characterised.

46) *Drosophila (Sophophora)* sp. D

Material examined: MALAWI: 2♂2♀, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991 (Lachaise) (MNHNP).

This species is very close to *curta* with respect to abdominal colouration, but differs in some minor characters of the male terminalia. It is presumably a new species, but we prefer delaying its description.

47) *Drosophila (Sophophora)* sp. E aff. *phyale* Tsacas

Material examined: MALAWI: 1♂, Zomba Plateau, 790 m, sweeping above fallen figs of *Ficus thonningii*, 7.iv.1991 (Lachaise) (MNHNP).

This individual unequivocally belongs to a new species of the *nikananu* complex (Tsacas & Chassagnard 1991). Its relationship with other species of this complex are unclear. On the basis of the tarsal sex-comb, which is short, it is closer to *nikananu* and *phyale* Tsacas, and more distant from *xanthia* Tsacas, of which the tarsal sex-comb is long. However, based on the male terminalia it is closer to *phyale* and *xanthia* – yet with differences in the surstylus prenisetae arrangement and aedeagus shape – and more distant from *nikananu*.

The specimen examined is rubbed and in poor condition; the antennae, one of the fore legs and one wing are lacking, while the second wing is damaged. The species is therefore not presently described.

Genus *Hirtodrosophila* Duda, 1923

This ancient subgenus of *Drosophila* was raised to the rank of genus by Grimaldi (1990). It is poorly represented in Africa and by only one species in the Malaŵi collection.

hirticornis group Burla, 195648) *Hirtodrosophila vina* Burla, 1954

Material examined: MALAWI-ZAMBIA: 20♂♀, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP); 17♂♀, *idem* but preserved frozen at -80°C for DNA analysis.

Distribution. Ivory Coast, Congo, Malaŵi (new record), Zambia (new record).

Genus *Liodrosophila* Duda, 1922

The genus is represented in the Afrotropical Region by 7 species including 3 from Madagascar.

In the course of study of the material from Malawi we examined *Drosophila lucida* Séguy, 1938. This species was included by Wheeler (1981) in the unclassified species, that is not assigned to any of the *Drosophila* subgenera. We now state that it belongs to the genus *Liodrosophila*, and thus establish a new combination as follows: *Drosophila lucida* Séguy, 1938 = *Liodrosophila lucida* (Séguy), **comb. n.**

The 4 continental species can be recognised as follows:

- 1 Scutum brown, silver shining punctate**argyrea** Tsacas
- Scutum glossy, black or rusty brown, not silvery punctate2
- 2 Scutum glossy, rusty brown, brown posteriorly**lucida** (Séguy)
- Scutum glossy black.....3
- 3 Legs entirely yellow.....**melania** (Séguy)
- Fore and mid femur, and at least apical third of hind femur black ...**lampra** Tsacas

49) *Liodrosophila lampra* Tsacas, 1990

Material examined: MALAWI-ZAMBIA: 1♂2♀, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP).

Distribution. South Africa (KwaZulu-Natal), Zimbabwe, Malawi (new record), Zambia (new record).

Genus *Lissocephala* Malloch, 1929

The genus *Lissocephala* presently includes 31 species inclusive of the three new species described below, and is distributed in the Oriental and Australasian (8 species) and mostly in the Afrotropical (23 species) Regions. Afrotropical species were separated in two clear-cut species groups: *juncta* and *sanu* (Tsacas & Lachaise 1979).

juncta group Tsacas & Lachaise, 1979

50) *Lissocephala bergi* Chassagnard & Tsacas, sp. n.

Figs 59–66, 84

Diagnosis. Close to *L. sosefi* sp. n. (see below), differing in the darkened costal cell, 10 rows of acrostichal setulae and some features of the terminalia.

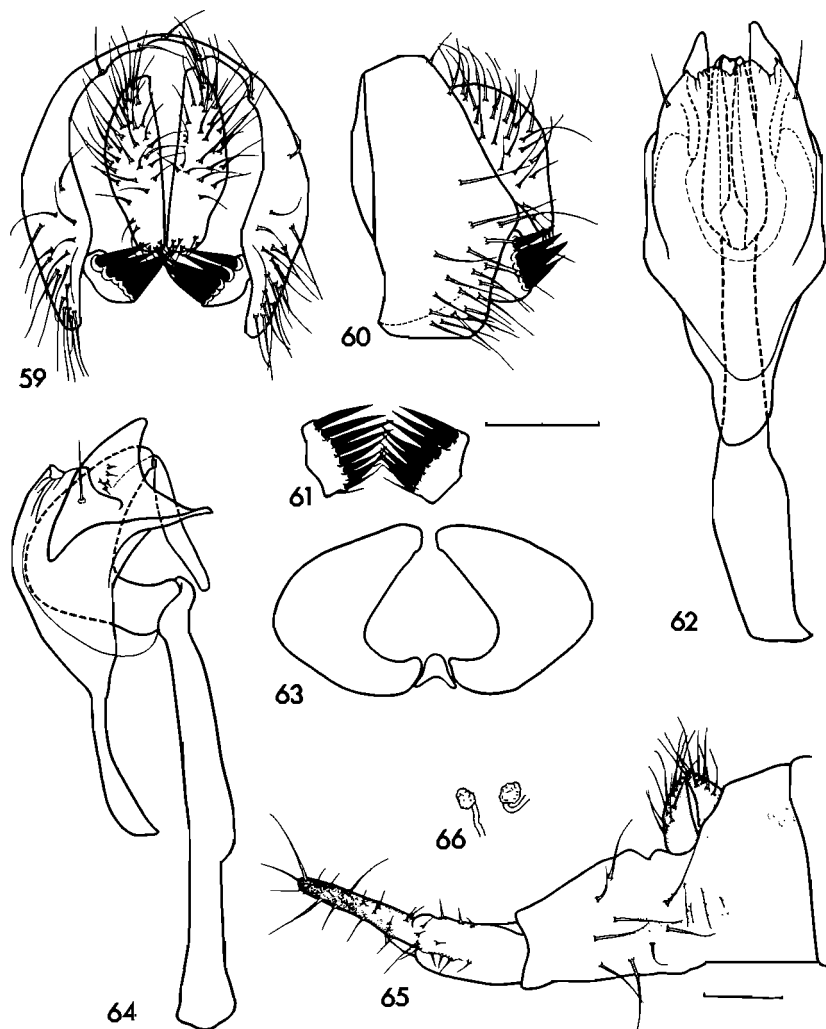
Male/Female:

Head. Frons as in *L. sosefi* but brown on upper part. Face with large facial carina. Arista with 4 dorsal and 2 ventral rays plus terminal fork.

Thorax. Scutum with 10 irregular rows of acrostichal setulae. Legs very pale. Wing: subapical wing patch varies in size, not reaching mid C3 section or extending beyond, costal cell brownish. Halter white.

Abdomen. Black with glints of copper.

Male terminalia. Epandrium widening gradually from dorsal edge to half height and narrowing slightly further down. A row of sparse, widely separated setae posterodorsally, a patch of dense setae posteroventrally; ventral edge truncated. Epandrial fragma narrow, slightly larger in the middle. Cercus narrow, narrowing dorsally and ventrally, covered with long setae becoming sparser on basal third, short



Figs 59–66. *Lissocephala bergi* Chassagnard & Tsacas sp. n. 59. Epandrium and associated structures, caudal view. 60. *idem*, lateral view. 61. Surstylus, posteroventral view. 62. Hypandrium and associated structures, ventral view. 63. *idem*, lateral view. 64. 'Distiphallus' in erection, caudal view. 65. Ovipositor. 66. Spermatheca. Scale: 0.1 mm.

and close-set setae on ventral edge. Surstylus oblique with comb-like row of 6–7 stout prensisetae accompanied by 4–5 long and strong setae. Hypandrium elongate, narrowed posteriorly, posterior edge 'wrinkled' with 3 major indentations, paramedian setae long and far between, in lateral view posterior third very narrow slightly bent anterodorsally. Anterior parameres triangular with group of 5 spinules in the middle; posterior parameres (aedeagus?) sickled-shaped. Aedeagal apodeme as long as hypandrium.

Ovipositor. Mid-length telescopic, postabdominal segments larger basally, tapering apically, egg guide narrow and dark.

Length (in mm): *Male*. Body 2.5; wing 2.3. *Female*. Body 2.9; wing 2.6.

Material examined: MALAWI: Holotype ♂, Zomba, Chancellor College, 790 m, sweeping above fallen figs of *Ficus sycomorus*, 9.iv.1991 (Lachaise) (MNHNP); Paratypes: 2♂3♀, *idem*; 1♂, *idem* but (NM). *Further material examined*: 4♂4♀, *idem*; preserved in alcohol for DNA analysis. IVORY COAST: 2♂1♀, (specimens registered 6854, 6855, and 6853 respectively in S. F. McEvey's file), Lamto, swept on *Ficus sur* figs, vi.1989 (Lachaise) (MNHNP). GUINEA: 7♂7♀, Mt. Nimba, 1220 m, Falls, ex *Ficus sur* figs, 29.iv.1993; 1♂1♀, *idem* but 725 m, Mifergi, swept on *Ficus artocarpoides*, 16.iv.1993 (Lachaise, Harry)(MNHNP). SOUTH AFRICA: 1♂, Port St Johns, *Ficus sur*, SR30, i.1989; 2 unsexed, *idem* but labelled F; 1♂, dissected, Grahamstown, *Ficus sur*, ii.1986; 1 unsexed, *idem* but labelled SR38, ex figs, em. 17.iii.1986; 2 unsexed, *idem* but labelled F5, SR44, 11.xii.1989; 1♂, *idem* but vi.1986, mature figs; 1 unsexed, *idem* but *Ficus natalensis*, SR40, iv.1985; 1 unsexed, Natal, Umhlanga, SR50, *Ficus thonningii*, 30.i.1990; 1 unsexed, Natal, Hibberdene, ex *Ficus lutea* figs, xii.1986; 2 unsexed, *idem* but SR39, *Ficus lutea* figs; 1 unsexed, Martindale, SR51, *Ficus ingens*, F2, emerged from figs, xii.1989; 1 unsexed, *idem* but em. 24.i.1990, C213, SR47 (Compton) (S.A.Museum).

Distribution. Malawi, Guinea, Ivory Coast, Kenya, South Africa.

Taxonomy. *L. bergi* belongs to the *juncta* species group.

Etymology. Species dedicated to Dr C. C. Berg, Director of the Norwegian Milde Arboretum and world specialist of *Ficus* and other Moraceae.

51) *Lissocephala kamundii* Chassagnard & Tsacas, sp. n.

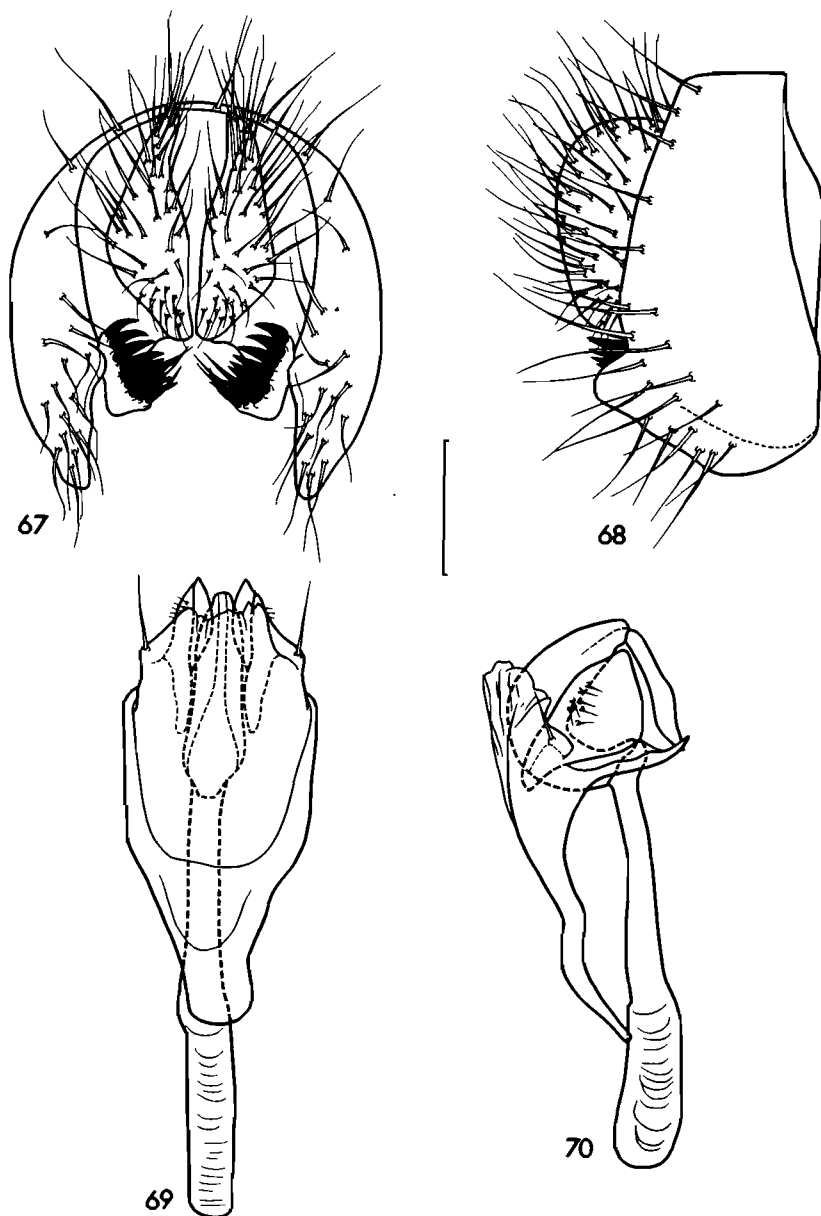
Figs 67–70, 82

Diagnosis. Large species close to *L. ambigua* Tsacas & Chassagnard, 1977; differing by frons colour more or less uniform in *ambigua* and by characters of male terminalia. As illustrations of *L. ambigua* terminalia were not published by Tsacas & Chassagnard (1977), we include them in the present work (Figs 71–74).

Male:

Head. Frons large and glossy, with clear-cut separation into 2 equal areas, upper part brown, lower part yellow. Fronto-orbital plate not much differentiated, located within brown part, *or*1 and *or*3 well developed, *or*2 like a short setula arising closer but more laterally set than *or*1. Ocellar triangle small and not much distinct, the 3 ocelli pale and accompanied by a black spot on their inner edge. Postocellar setae developed and convergent. Face glossy greyish-white, facial carina wide, triangular and flattened. Clypeus short and wide, concolorous with face. Palpus yellow with an apical seta accompanied by a few marginal unequally-sized setulae. Antenna yellow, arista with 5 dorsal and 3 ventral rays plus terminal fork. Eyes red. Gena wide white-yellowish.

Thorax. Glossy and rusty yellow. Scutum with 8 rows of acrostichal setulae. Basal and subapical scutellar setae subequal, the former parallel or slightly convergent, the latter hardly crossed. Legs paler than thorax. Wings: costal cell entirely brown, radial cell 1 with large brown band anteriorly leaving a gap by R_{2+3} vein on its basal two-thirds, subapical wing patch clearly disjunct from band. Halter with white-yellowish stem and white capitulum.



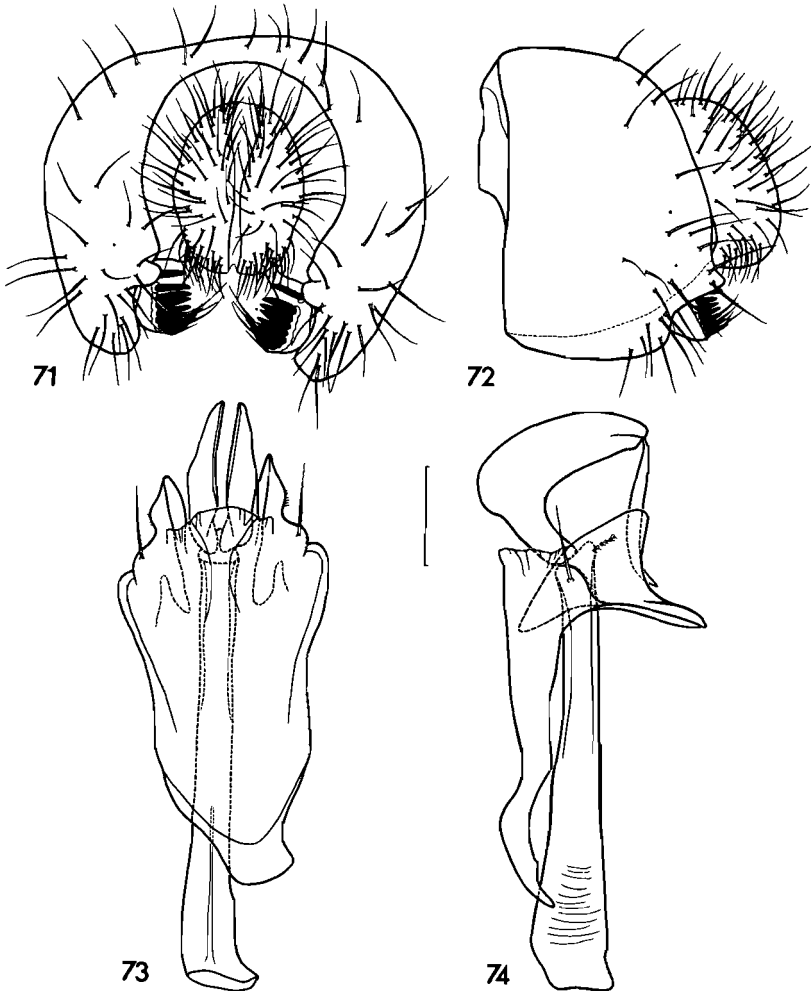
Figs 67–70. *Lissocephala kamundii* Chassagnard & Tsacas sp. n. 67. Epandrium and associated structures, caudal view. 68. *idem*, lateral view. 69. Hypandrium and associated structures, ventral view. 70. *idem*, lateral view. Scale: 0.1 mm.

Abdomen. Glossy brown with glints of copper.

Male terminalia. Epandrium large, rounded ventrally, making a small globose expansion posteroventrally following an inflexion of posterior epandrial edge; along this is a row of long setae doubled and closer-set ventrally; epandrial fragma narrow,

slightly conical. Cercus narrow ventrally and stretching dorsally bearing numerous long setae, except ventrally where they are short and close-set. Surstylus elongate, ventral edge rectangular, jaw-like, bearing comb-like row of long stout prenisetae incurved ventro-interiorly, accompanied by 3 longer strong setae internally. Hypandrium with its posterior edge 'wrinkled', appearing elongate in ventral view with narrowed novasternum, paramedian setae long and most laterally, in lateral view presents an inflexion in its anterior third, novasternal end bent dorsally. Anterior parameres oblong with 6 setulae in a patch; posterior parameres (aedeagus?) crescent-shaped. Aedeagal apodeme as long as hypandrium.

Female: Unknown.



Figs 71–74. *Lissocephala ambigua* Tsacas & Chassagnard, 1977. 71. Epandrium and associated structures, caudal view. 72. *idem*, lateral view. 73. Hypandrium and associated structures, ventral view. 74. *idem*, lateral view. Scale: 0.1 mm.

Length (in mm): *Male*. Body 3.8; wing 2.8.

Material examined: MALAWI: Holotype ♂, Zomba, Chancellor College, 790 m, sweeping above fallen figs of *Ficus sycomorus*, 10.iv.1991 (Lachaise) (MNHNP); Paratype, 1♂, *idem*.

Distribution. Malaŵi.

Taxonomy. *L. kamundii* belongs to the *juncta* species group.

Etymology. Species dedicated to D. A. Kamundi, botanist at the National Herbarium and Botanic Gardens, Zomba, Malaŵi.

52) *Lissocephala sosefi* Chassagnard & Tsacas, sp. n.

Figs 75–81, 83

Diagnosis. Subapical wing patch isolated. Thorax pale, abdomen dark with glints of copper.

Male/Female:

Head. Frons glossy, yellow anteriorly, brownish posteriorly, with large median band. Fronto-orbital plate not much differentiated, *or1* and *or3* well developed and subequal, *or2* like a short setula arising closer but more laterally set than *or1*. Ocellar triangle small and not much distinct. Postocellar setae crossed. Face glossy greyish-white, facial carina wide, triangular and flattened. Clypeus and palpus yellowish. Antenna rusty yellow, arista with 4 dorsal and 2 ventral rays plus terminal fork. Eyes dull brick. Gena concolorous with lower frons.

Thorax. Glossy and rusty. Scutum with 8 rows of acrostichal setulae. Basal scutellar setae parallel or slightly divergent, subapical scutellar setae crossed. Legs paler than thorax. Wing hyaline, subapical wing patch isolated, extending to R_{2+3} posteriorly and not reaching half $c3$ section basally. Halter white.

Abdomen. Dark brown with glints of copper.

Male terminalia. Epandrium large, ventral edge truncated, posterior edge with sparse widely separated setae except posteroventrally where they are dense and close-set, posterior edge doubly inflexed in its ventral half; anteroventral angle pointing forwards. Terminalia of holotype (the only male available), is in erection, and therefore the description of anterior parameres is not possible; posterior parameres (aedeagus?) crescent-shaped, swollen medially. Aedeagal apodeme almost 1.5 times as long as hypandrium.

Ovipositor. Mid length telescopic postabdominal segments, thick-set, almost cylindrical, egg guide massive, knife-edged and dark.

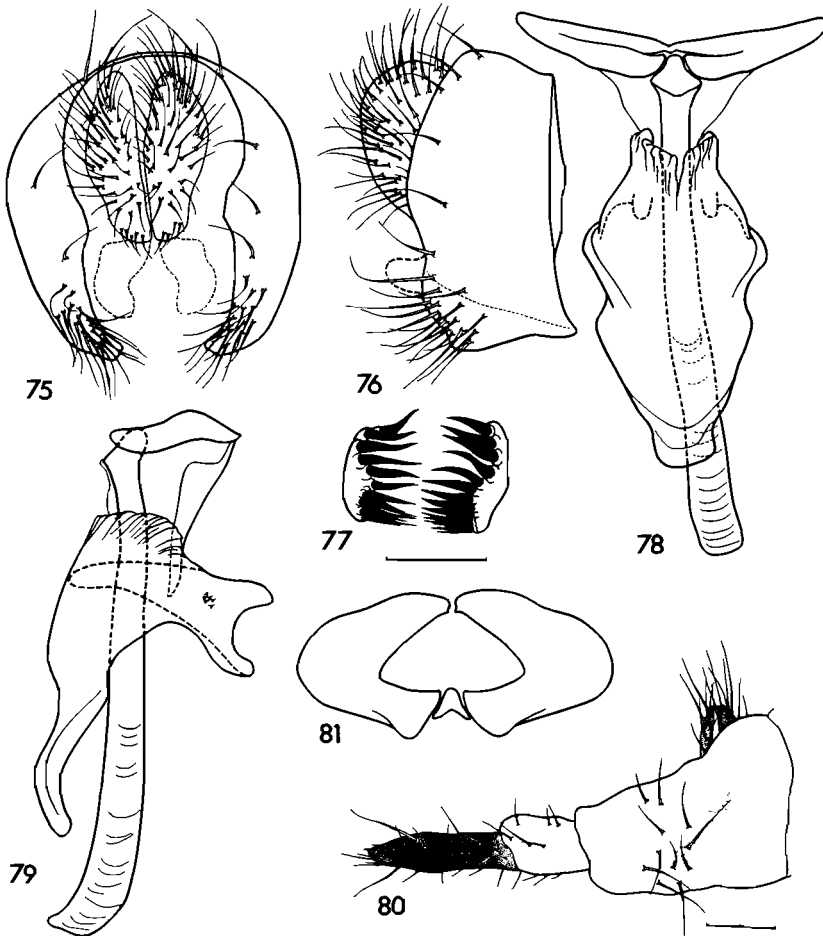
Length (in mm): *Male*. Body 3.0; wing 2.6. *Female*. Body 2.7; wing 2.3.

Material examined: MALAWI: Holotype ♂: Zomba, Chancellor College, 790 m, sweeping below *Ficus sycomorus*, 9.iv.1991 (Lachaise) (MNHNP); Paratypes, 2♀, *idem* but 9.iv.1991 (MNHNP). *Further material examined*: 1♂4♀, *idem* but preserved in alcohol for DNA analysis.

Distribution. Malaŵi.

Taxonomy. *L. sosefi* belongs to the *juncta* species group.

Etymology. The species name is dedicated to Dr. M. S. M. Sosef from the Wageningen Agricultural University.



Figs 75–81. *Lissocephala sosefi* Chassagnard & Tsacas sp. n. 75. Epiandrium and associated structures, caudal view. 76. *idem*, lateral view. 77. Surstylus. 78. Hypandrium and associated structures in erection, ventral view. 79. *idem*, lateral view. 80. 'Distiphallus' in erection, apical view. 81. Ovipositor. Scale: 0.1 mm.

53) *Lissocephala* sp. A

Material examined: MALAWI: 2 ♀, Zomba, Chancellor College, 790 m, sweeping below *Ficus thonningii*, 4.iv.1991 (Lachaise) (MNHNP).

The lack of the male prevents unequivocal identification of the species.

54) *Lissocephala* sp. B

Material examined: MALAWI: 1 ♀, Kasungu National Park, 28.iii.1991 (Lachaise) (MNHNP).

The lack of the male prevents unequivocal identification of the species.

sanu group Tsacas & Lachaise, 197955) *Lissocephala couturieri* Tsacas & Lachaise, 1979

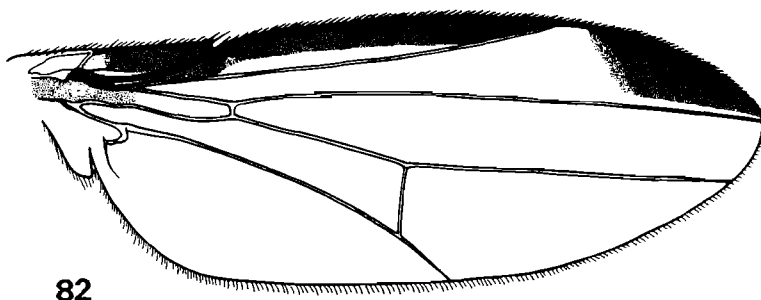
Material examined: MALAWI: 20♂♀, Zomba, Chancellor College, 790 m, sweeping above fallen figs of *Ficus sycomorus*, 5–10.iv.1991; 5♂♀, *idem* but below *Ficus thonningii*, 4.iv.1991 (Lachaise) (MNHNP). *Further material examined*: 90 specimens (including 20♂22♀, and 48 unsexed), *idem* but 4–6.iv.1991, in alcohol for DNA analysis.

Distribution. Ivory Coast, Malaŵi (new record).

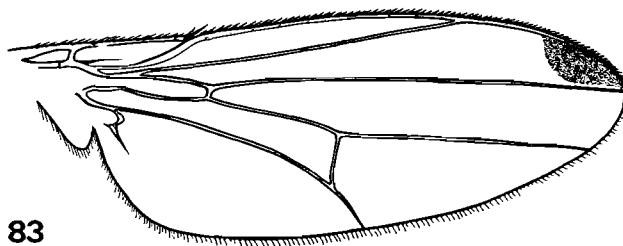
56) *Lissocephala lebou* Tsacas & Lachaise, 1979

Material examined: MALAWI: 2♂2♀, Zomba, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 4.iv.1991 (Lachaise) (MNHNP).

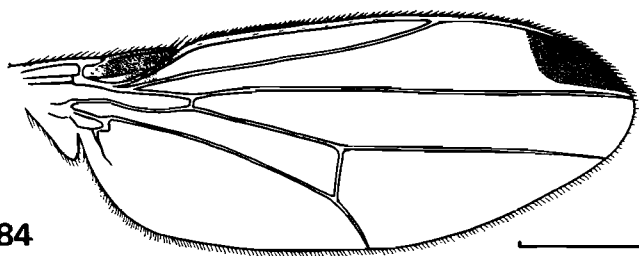
Distribution. Senegal, Malaŵi (new record).



83



84



Figs 82–84. Right wing of *Lissocephala* species. 82. *L. kamundii* Chassagnard & Tsacas sp. n. 83. *L. sosefi* Chassagnard & Tsacas sp. n. 84. *L. bergi* Chassagnard & Tsacas sp. n. Scale: 0.5 mm.

Genus *Mycodrosophila* Oldenberg, 1914Subgenus *Mycodrosophila*

Only the subgenus *Mycodrosophila* s. str. is present in Africa, with 15 species including the two new species from Malawi described here.

Key to southern African species of *Mycodrosophila* (*Mycodrosophila*)

- 1 Pleura dark or black; femur entirely or with at least basal three-quarters black....2
- Pleura pale or with slight brown band across; femur pale3
- 2 Abdomen: T1 brownish-yellow, T3–T4 with pale spots, one on each side. Terminalia as in Figs 51–54 (Tsacas 1990).....**melanophaea** Tsacas
- Abdomen: T1 black with small pale, whitish-pollinose spot on each side, T3–T4 black. Terminalia as in Figs 90–95.....**nigrans** Chassagnard & Tsacas, sp. n.
- 3 Pleura entirely white, wings without transverse brown band....**fracticosta** (Lamb)
- Pleura white, brown banded across, wings without transverse brown band4
- 4 Wings brown without transverse spots. Terminalia as in Figs 85–89**dudleyi** Chassagnard & Tsacas, sp. n.
- Wings hyaline with 2 brown transverse spots, one extending down the lappet, the other at level of humeral break. Terminalia as in Figs 55–56 (Tsacas 1990).....**punctata** Tsacas

57) *Mycodrosophila* (*Mycodrosophila*) **dudleyi** Chassagnard & Tsacas, sp. n.

Figs 85–89

Diagnosis. Characterised by lighter postpronotum, abdominal spots and mostly by the complex male terminalia.

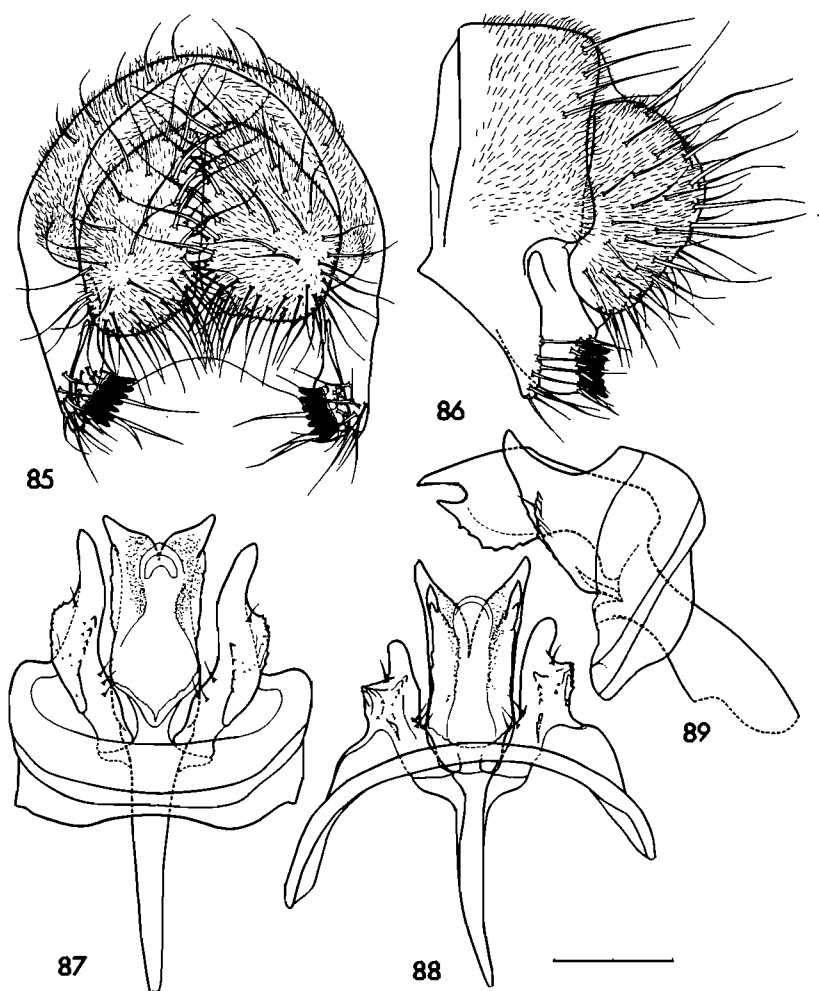
Male:

Head. Frons black with a round rusty yellow spot anteriorly, entirely silver pollinose. Fronto-orbital plate glossy black, *or*1 and *or*3 subequal, *or*2 similar to a short setula. Ocellar triangle glossy black. Postocellar setae short and crossed. Antenna: pedicel rusty-brown, flagellum brown, arista with 4 dorsal (strongly bent) and 2 ventral rays plus terminal fork. Face greyish, turning brown anteriorly; facial carina contrasted, non-existent basally between antennae, greyish with ridge paler. Epistome brown, darker laterally. Clypeus black. Palpus black with long apical seta. Gena widened posteriorly, whitish, darkened anteriorly, silvery pollinose. Eye dull orange red.

Thorax. Scutum glossy black with pale brown postpronotal lobe, 10–12 rows of acrostichal setulae, 1 single pair of dorsocentral setae, inserted at posterior extreme. Scutellum black non-glossy, basal scutellar setae short and hardly convergent, apical scutellar setae long and crossed. Pleura whitish with brown band from halter base to anepisternum. Anatergite black. 2 katepisternal setae, anterior very short and slender. Legs generally pale, coxa and trochanter concolorous with pleura, femora yellow, tibiae and tarsomeres rusty. Wing brown, veins paler, lappet black. C-index = 1.6. Halter with whitish stem and black capitulum.

Abdomen. Black except T1 and proximal half of T2 yellow and slightly darkened

laterally, T5 with 2 paramedian spots yellow and silvery pollinose, T3–T6 with narrow yellow zone along lateral edges.



Figs 85–89. *Mycodrosophila dudleyi* Chassagnard & Tsacas sp. n. 85. Epandrium and associated structures, caudal view. 86. *idem*, lateral view. 87. Hypandrium and associated structures, ventral view. 88. *idem*, anteroventral view. 89. *idem*, lateral view. Scale: 0.1 mm.

Male terminalia. Epandrium broad, bearing on each side 4–5 long marginal setae dorsally covered with dense pollinosity, leaving bare a narrow anterior band; ventral epandrial extension toe-like, bearing 8–9 long setae posteroventrally. Epandrial fragma narrow. Cercus bulky and broad, entirely covered with dense pubescence and bearing a number of long setae, shorter and closer-set ventrally, more especially interno-ventrally. Surstylus elongate, bearing 7–8 strong prenisetae arranged in a comb-like row internally, comb accompanied by 3 long setae internally, and 12 shorter setae externally. Hypandrium more or less bat-shaped, narrow, lateral

extensions bent posteriorly, posterior edge straight without paramedian setae. 2 complex, strongly developed structures attached to novasternum are considered to be parameres; these are finger shaped, wide basally, progressively narrower apically, serrulate laterally and ventrally, bearing short setula in notch at level of posterior third externally, and a group of 3 other setulae on inner edge at level of anterior third. Aedeagus with complex structure, distiphallus bifid, each branch presenting a deep subapical notch posteroventrally, serrated dorsally.

Female: Unknown.

Length (in mm): *Male*. Body 2.7; wing 2.6.

Material examined: MALAWI-ZAMBIA: *Holotype* ♂, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHN); *Paratypes*, 2♂, *idem* (MNHN), one more ♂ in poor state, *idem*, excluded from paratypes; 1♂, *idem* but (NM).

Distribution. Malawi, Zambia. See comments for *Drosophila seyanii*.

Taxonomy. *M. dudleyi* belongs to the subgenus *Mycodrosophila*; the aedeagal structure of the terminalia places it at some distance from all known African species, however the epandrium and surstylus are very close to that of *nigrans* sp. n.

Etymology. The species name is dedicated to Dr. Cornell O. Dudley, who did much for promoting entomology in Malawi.

58) *Mycodrosophila* (*Mycodrosophila*) *nigrans* Chassagnard & Tsacas, sp. n.

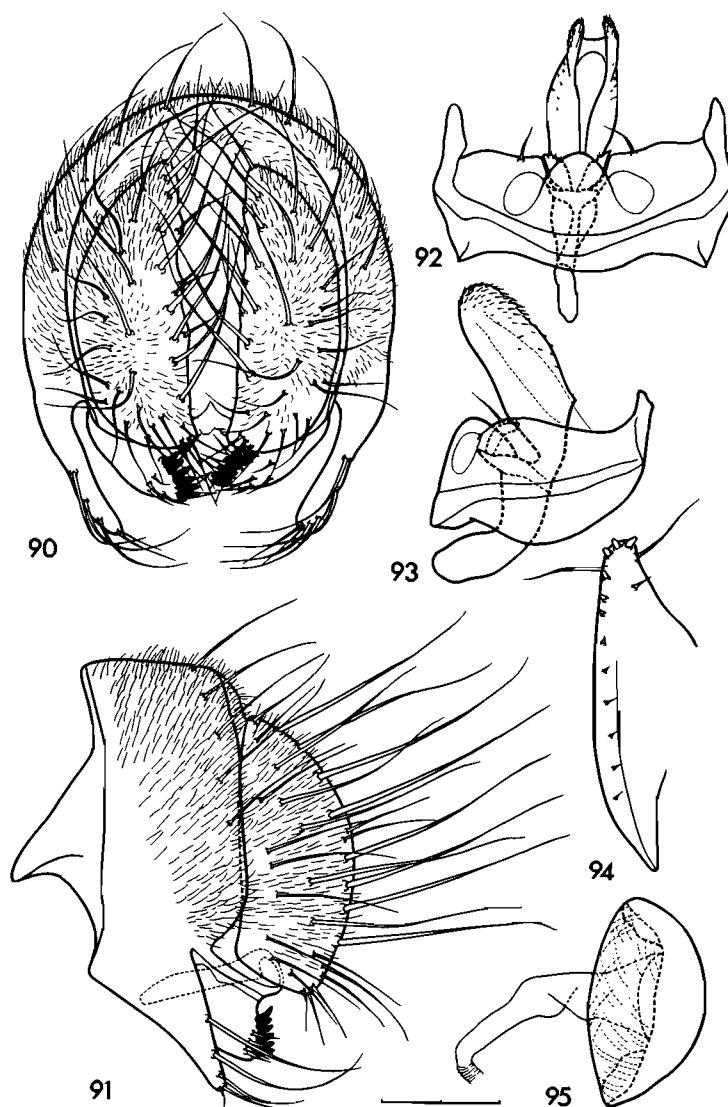
Figs 90–95

Diagnosis. Entirely black except anterior part of scutum paler and apical quarter of femora brownish-yellow. Wings with short brown band across, extending across lappet posteriorly and ending in middle of cell M.

Male/Female:

Head. Frons bronze blackish-brown, with fine pollinosity visible at certain angles. Fronto-orbital plates short and glossy black, *or1* and *or3* subequal, *or2* if present similar to short setula. Ocellar triangle small and black. Face black, facial carina contrasted, the ridge of which is flattened in its lower third, epistome wide and glossy, 1 vibrissa. Clypeus deep dark and glossy. Antenna dark brown, arista with 4 dorsal and 2 ventral rays plus terminal fork. Palpus black with long apical seta. Gena wide and blackish. Eye purplish-red.

Thorax. Scutum bulging, brown, paler anteriorly on each side of similarly brown medial band. 1 pair dorsocentral setae (anterior pair lacking). 8–10 irregular rows of acrostichal setulae. Scutellum short, bulging, concolorous with posterior scutum but less glossy, covered with slightly golden pollinosity. Basal scutellar setae short (about half apical ones) and slightly convergent, apical scutellar setae long and crossed. Anatergite brown. Pleura glossy black, katepisternal setae: anterior short and slender, posterior strong and long. Legs: coxae black, femora dark turning markedly paler distally, rest of legs slightly darkened yellow. Wing brown, veins darker with black band across, extending over lappet posteriorly and reaching middle of basal radial cell; on distal medio-cubital cell is also a faint brown spot. C-index, male = 1.3, female = 1.2. Halter with white stem and brown capitulum.



Figs 90–95. *Mycodrosophila nigrans* Chassagnard & Tsacas sp. n. 90. Epandrium and associated structures, caudal view. 91. *idem*, lateral view. 92. Hypandrium and associated structures, ventral view. 93. *idem*, lateral view. 94. Ovipositor. 95. Spermatheca. Scale: 0.1 mm.

Abdomen. Entirely glossy black with 2 small pale paramedian spots on T5 anteriorly; on T1 are also 2 small oblong white pollinose spots laterally.

Male terminalia. Epandrium relatively narrow with epandrial fragma pointing anteriorly at nearly half height, bearing on each side 5 long marginal setae dorsally and short pubescence on its dorsolateral two-thirds. Ventral epandrial extension narrow, toe-like, bearing 3–4 long setae and 2 short setae posteroventrally. Cercus bulky, almost entirely covered with dense pollinosity and bearing a number of long setae, shorter and closer set interno-ventrally. Surstylus elongate, oblique, with 6–

strong prensisetae accompanied by 3 strong setae internally and 4–5 short setae externally. Hypandrium strikingly short and stocky, posterior edge making a notch on each side of medial extension, rounded, of novasternum; lateral extensions pointing posteriorly. Paramedian setae short and widely separated. Aedeagus and aedeagal apodeme structure boomerang-shaped and the extremities of which point ventrally; distiphallus bifid and sugar-tong shaped, spinulate posterodorsally. Parameres small, sulcate dorsally, bearing 6 sensilla each.

Ovipositor. Characterised by 2 very long apical setae, one pointing dorsally, the other ventrally; tapering posteriorly, 3 strong apical blunt teeth followed by 9 shorter ones ventrally, changing gradually from teeth to setulae. Spermatheca large, mushroom-like.

Length (in mm): Male. Body 3.0; wing 3.1. Female. Body 3.3; wing 3.4.

Material examined: MALAWI-ZAMBIA: Holotype ♂, Nyika Plateau, Chowo forest, 2120 m, 14.iv.1991 (Lachaise) (MNHNP); Paratypes, 8♂6♀, *idem* (MNHNP); 1♂1♀, *idem* but (NM).

Distribution. Malaŵi, Zambia.

Taxonomy. This species belongs to the *nigerrima* complex (Burla 1954) based on the entirely brown pleura. It is quite close to the 'Abweibchende Form' of *M. nigerrima sensu* Burla, but differs in characters of the surstylus and aedeagus. Despite it belonging to the *nigerrima* complex, it has close affinities with *M. punctata* Tsacas from KwaZulu-Natal (South Africa) due to similar yet less marked abdominal spots and especially the male terminalia. The following species are classified in the *nigerrima* complex: *nigerrima* Lamb (Seychelles and presumably Ivory Coast), *melanophaea* Tsacas (South Africa), *nigrans* sp. n. (Malaŵi), and the two species described but not named by Burla (1954).

Etymology. From Latin, alluding to the dark body colour of the species.

Genus *Scaptodrosophila* Duda, 1923

This genus has long been considered a subgenus of *Drosophila*, and was raised to the rank of genus by Grimaldi (1990). Although this genus is well represented in Africa with more than 20 species, it is somewhat depauperate in the present Malaŵi collection which is composed of 4 species, including one new one. Species have long been known to visit mostly the sap of a diversity of palm tree species (Burla 1955, Lachaise & Tsacas 1983); in Malaŵi these feeding/breeding sites were poorly examined.

aterrima group Tsacas & Chassagnard, 1988

59) *Scaptodrosophila caliginosa* (Lamb, 1914)

Material examined: MALAWI: 2♂1♀, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Seychelles, Chad, Cape Verde Islands, Senegal, Gambia, Ivory Coast, Ghana, Nigeria, Cameroun, Congo, Madagascar, South Africa, Mauritius, Malaŵi (new record).

60) *Scaptodrosophila smicra* (Tsacas, 1980)

Material examined: MALAWI: 16♂♀, Kasungu National Park, Lifupa Pond, 990 m, in flowers of *Hibiscus panduriformis* Burm. f., 27.iii.1991 (Lachaise) (MNHNP).

Distribution. Kenya, Guinea, Ivory Coast, Congo, Malaŵi (new record).

latifasciaeformis group Burla, 1954*latifasciaeformis* subgroup61) *Scaptodrosophila dibi* (Burla, 1954)

Material examined: MALAWI: 1♂3♀, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Ivory Coast, Cameroun, Gabon, Kenya, Burundi, Zimbabwe, South Africa, Malaŵi (new record).

62) *Scaptodrosophila latifasciaeformis* (Duda, 1940)

Material examined: MALAWI: 1♂, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 1♂, Zomba, 790 m, below *Ficus sycomorus*, 8.iv.1991 (Lachaise) (MNHNP). A series of wild-caught females from Zomba was used to found one multifemale line.

Distribution. Uganda, Ethiopia, Senegal, Gambia, Ivory Coast, Togo, Benin, Nigeria, Cameroun, Central African Republic, Gabon, Congo, Rwanda, Burundi, Madagascar, Rodriguez, Seychelles, Malaŵi (new record).

mokonfim subgroup63) *Scaptodrosophila lambi* (Duda, 1940)

(sensu Burla 1954)

Material examined: MALAWI: 1♂, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991 (Lachaise) (MNHNP).

Distribution. Seychelles, Ivory Coast, Cameroun, Central African Republic, Uganda, Malaŵi (new record).

ungrouped species

64) *Scaptodrosophila melaena* Chassagnard & Tsacas, sp. n.

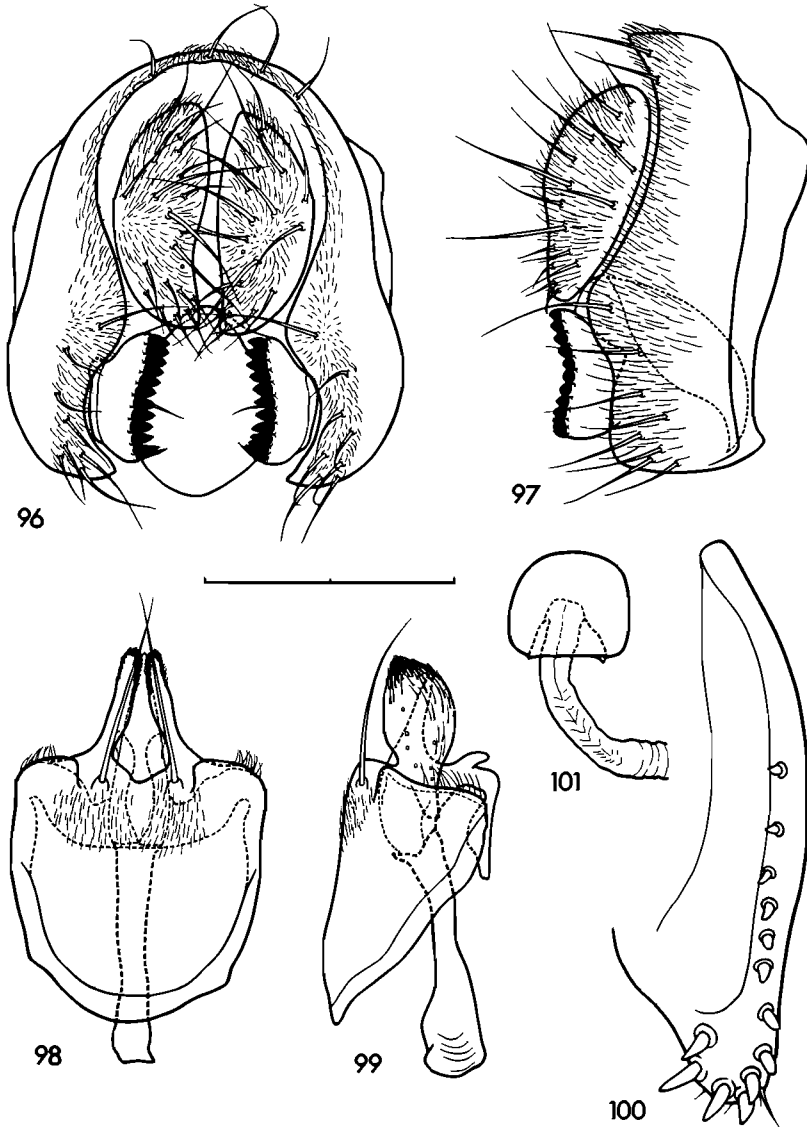
Figs 96–101

Diagnosis. Small, entirely glossy black, except for tibiae and tarsi.

Male/Female:

Head. Frons black except transverse band rusty brown, extending up between fronto-orbital plates and tip of ocellar triangle. Fronto-orbital plates and ocellar triangle glossy black. Orbital setae well developed, *or1* and *or3* subequal, *or2* about half *or1* and more laterally set, and at level of this latter seta. Postocellar setae small and crossed. Antenna black except pedicel rusty brown, arista with 4 dorsal, strongly bent apically, and 2 ventral rays plus terminal fork. Face brown, carina narrow.

Thorax. Entirely black and glossy. 6 rows acrostichal setulae. 3 katapisternal setae,



Figs 96–101. *Scaptodrosophila melaena* Chassagnard & Tsacas sp. n. 96. Epandrium and associated structures, caudal view. 97. *idem*, lateral view. 98. Hypandrium and associated structures, ventral view. 99. *idem*, lateral view. 100. Ovipositor. 101. Spermatheca. Scale: 0.1 mm.

anterior and mid ones subequal, posterior one compared to mid one is stronger and bent. Legs: femora black, tibiae paler. Wings brownish, veins brown, *c*-index, male = 1.4, female = 1.6. Halter pale yellow.

Abdomen. Glossy black.

Male terminalia. Epandrium wider ventrally, posterior edge swollen at level of ventral end of cercus, and bearing on each side 2 dorsal and 8 ventral setae. Posterior half of epandrium densely pubescent. Ventral epandrial extension truncated. Anterior

epandrial fragma narrow. Surstylus developed with a long comb on innermost edge, sulcate inwards, and composed of 10–11 strong and short teeth plus one seta-like tooth ventrally. Cercus broad, becoming narrower ventrally, densely pollinose, and bearing long setae, shorter and finer ventrally. Decasternum ovoid. Hypandrium wide, almost square, pollinose on posterior edge and on posterolateral angles, posterior edge indefinite, paramedian setae very long, reaching over distiphallus and far between; parameres swollen laterally and pubescent posterodorsally, with many sensilla; distiphallus pointing posterodorsally and ending at level of parameres.

Ovipositor. Elongate, tapering posteriorly, 3 strong apical blunt teeth followed anteriorly by 1 fine ventral seta and 9 shorter teeth of decreasing size ventrally; beside the first apical tooth is an additional inner and shorter one. Spermatheca globose.

Length (in mm): Male. Body 1.9; wing 1.7. Female. Body 1.8; wing 1.8.

Material examined: MALAWI: Holotype ♂: Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP); Paratypes, 2♂, *idem*; 2♂, Zomba Plateau, Chancellor College, 790 m, sweeping above fallen figs of *Ficus thonningii*, 6.iv.1991 (Lachaise) (MNHNP); 1♂, *idem* but (NM); 1♀, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (NM).

Distribution. Malawi.

Taxonomy. *Scaptodrosophila melaena* cannot be assigned to any of the African species groups of the genus *Scaptodrosophila* described by Burla (1954). The lack of prescutellar setae and its small size place it apart from the *saba* group. The 6 rows of acrostichal setulae and the lack of prescutellars do not allow inclusion in the *latifasciaeformis* group. In terms of its male terminalia the epandrium and associated elements are definitely close to those of *S. triangulifer* (Lamb), and the hypandrium and associated elements are reminiscent of those of *S. xiphiochaeta* Tsacas & Chassagnard, 1990. A third species, *S. adyukru* (Burla), only known from females, shares with *S. xiphiochaeta* the lack of *or1* and prescutellar setae. From these considerations it appears reasonable not to include *S. melaena* in any of the previously described species groups; neither would it be reasonable to erect a new species group without more information.

Etymology. From Greek, μέλας, μέλαινα, = black, alludes to the dark body colour of the species.

Genus *Zaprionus* Coquillett, 1902

Subgenus *Zaprionus*

armatus group Chassagnard & Tsacas, 1993

tuberculatus subgroup Chassagnard & Tsacas, 1993

65) *Zaprionus (Zaprionus) sepsoides* Duda, 1939

Material examined: MALAWI: 8 specimens (ex strain), Lilongwe, 20.iv.1991 (Lachaise) (MNHNP).

Distribution. Subsaharan Africa: Uganda, Ivory Coast, Cameroun, Central African Republic, Gabon, Congo, Zambia, Madagascar, South Africa, Comoro, Malawi (new record).

66) *Zaprionus (Zaprionus) tuberculatus* Malloch, 1932

Material examined: MALAWI: 8 specimens (ex strain), Lilongwe, 20.iv.1991 (Lachaise) (MNHNP).

Distribution. All over sub-Saharan Africa: Zimbabwe, Cape Verde, Madagascar, St Helena, Réunion, Mauritius, Rodriguez, Comoro, Seychelles, Malawi (new record), Canary Islands, Egypt, Cyprus. This basically afrotropical species has extended its geographical range not only to the Indian Ocean islands and afrotropical Atlantic islands, but also to palaearctic circum-mediterranean islands and continental areas.

Zaprionus (Zaprionus) spp.

Material examined: MALAWI: 7♀ of the *tuberculatus* subgroup from various localities, Lilongwe, Kasungu, Luwawa, could not be identified; they presumably belong to the two above-mentioned (MNHNP) species: *sepsoides* and *tuberculatus*.

vittiger subgroup Chassagnard & Tsacas, 199367) *Zaprionus (Zaprionus) camerounensis* Chassagnard & Tsacas, 1993

Material examined: MALAWI: 2♂, Lilongwe, 20.iv.1991 (Lachaise) (MNHNP).

Distribution. Cameroun, Malawi (new record).

68) *Zaprionus (Zaprionus) indianus* Gupta, 1970

Material examined: MALAWI: 27♂♀, Zomba, Chancellor College, 790 m, above fallen figs of *Ficus thonningii*, 6.iv.1991; 5♂♀, *idem* but above fallen figs of *Ficus sycomorus*; 7♂♀, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 11♂♀, Lilongwe, 20.iv.1991; 15♂♀, Kasungu National Park, 28.iii.1991; 19 unsexed, Vipha Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991; (Lachaise) (MNHNP). Series of wild-caught females were used to found 7 multifemale, 24 multifemale, 3 isofemale and 1 multifemale lines from Lilongwe, Kasungu and Nyika-Chilinda respectively.

Distribution. India; all over Subsaharan Africa: Madagascar, St Helena, Réunion, Mauritius, Comoro, Seychelles, Malawi (new record), Canary Islands, Saudi Arabia.

Z. indianus is the most common and widespread species in Africa. This afrotropical species is assumed to have extended its geographical range to India for a few decades and has become common there, and more recently to the Canary Islands.

69) *Zaprionus (Zaprionus) proximus* Collart, 1937

Material examined: MALAWI: 7♂, Vipha Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

These specimens are the first to be assigned to this species since its description.

Distribution. Kenya, Malawi (new record).

70) *Zaprionus (Zaprionus) sp. B aff. proximus*

Material examined. MALAWI: 3♂, Vipha Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

71) *Zaprionus (Zaprionus) spinipilus* Chassagnard & McEvey, 1992

Material examined: MALAŴI: 8♂, Nyika Plateau, Chilinda, 2250 m, 15–16.iv.1991; 2♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP). ETHIOPIA: 1♂, Addis Ababa, light trap, x.1955 (Lane) (USNM, Washington).

Distribution. Madagascar, Cameroun, Malaŵi (new record), Ethiopia (new record).

72) *Zaprionus (Zaprionus) sp. A aff. spinipilus*

Material examined: MALAŴI: 1♂, Zomba, banana trap, secondary growth, 720 m, 5.iv. 1991; 8♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

73) *Zaprionus (Zaprionus) taronus* Chassagnard & Tsacas, 1993

Material examined: MALAŴI: 2♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. Gabon, Malaŵi (new record).

74) *Zaprionus (Zaprionus) sp. C aff. taronus*

Material examined: MALAŴI: 1♂, Zomba, banana trap, secondary growth, 790 m, iv.1991; 2♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

75) *Zaprionus (Zaprionus) vittiger* Coquillett, 1902

Material examined: MALAŴI: 1♂, Viphya Plateau, Luwawa Forest Reserve, Luwawa Pond, *Pinus* spp. forest, 1500 m, 29.iii.1991 (Lachaise) (MNHNP).

Distribution. South Africa, Malaŵi (new record).

inermis group Chassagnard & Tsacas, 199376) *Zaprionus (Zaprionus) ghesquierei* Collart, 1937

Material examined: MALAŴI: 1 unsexed, Zomba Plateau, Chancellor College, 790 m, above fallen figs of *Ficus thonningii*, 6.iii.1991; 5 unsexed, Cape Maclear, dry ravine, *Brachystegia* woodland, 30.iii.1991; 7 specimens, Lilongwe, 20.iv.1991; 5 specimens, Kasungu National Park, 990 m, 27.iii.1991 (Lachaise) (MNHNP). Two wild-caught females from Lilongwe and two others from Kasungu were used as foundresses of 4 isofemale lines.

Distribution. Zaïre, Senegal, Ivory Coast, Benin, Nigeria, Cameroun, Congo, Kenya, Tanzania, Madagascar, South Africa, Malaŵi (new record), Cyprus, Turkey. Presumably this afrotropical species has extended its geographical range to eastern Mediterranean areas in very recent times.

DISCUSSION

The natural vegetation of extensive areas of Malaŵi is normally *Brachystegia* woodland with *Acacia* and *Combretum* in more fertile areas. The *miombo* woodland (*Brachystegia* spp., *Julbernadia* spp., *Isobertinia* spp.) extends southwards to the

Limpopo River indicating that it formerly covered much of the middle altitude of the Southern Region (J. Leonard, J. Timberlake, *pers. comm.*). Such extensive vegetation formation would not *a priori* have appeared much suitable to Drosophilidae, and therefore presumably poor attention has hitherto been paid to such phytogeographic areas by drosophilists. In fact this investigation is the first devoted to Malawi for this group of insects and it definitely appears that Malawi is unexpectedly speciose for Drosophilidae. We report here the presence of 11 genera comprising 14 subgenera, and 26 species groups including 29 species subgroups and 76 species (Table 3).

Unlike vertebrates and possibly well-known insect families, the notion of endemism is uncertain for many other insect families including drosophilids, of which the distributions are incompletely known. This is particularly true of speciose tropical faunas and floras where new taxa are frequently found. Whenever such new taxa are discovered, the question arises as to whether or not the new taxon will remain the local endemic it appears first to be. It nonetheless remains that for the overall Malawi collection there are 16 new species described and 5 more species suspected to be new taxa among 76 recorded, that is from 21 to 28 % of putative local endemic species (Table 4). Still more locally, 5 of the 15 species from Nyika are new (33 %). If we consider the small Chowo forest patch alone, 4 of the 11 species are new, that is 36 % of the fauna.

Table 5 summarises the biogeographic affinities of the 56 taxa which were assigned a species name. It appears that Malawian drosophilids have affinities with eastern, southeastern and western Africa, and the Indian Ocean islands. As a result, Malawi seems to be a crossroads, resulting from a diversity of migration events.

Sampling and community composition (Fig. 102)

The number of days of capture of Drosophilidae was unequal depending on the localities, that is two days at Cape Maclear and Lilongwe, four days on the Vipha (Luwawa) and Nyika (Chilinda+Chowo) Plateau, five days at Kasungu, and ten days on the Zomba Plateau. However, the effort of capture per collecting day (i.e. number of traps, nature of bait, duration of sweeping around traps) was consistent enough to allow attempting some correlations. If the number of new species increases significantly with both the number of species and the number of genera ($r = 0.91$ and 0.83 respectively, $P < 0.05$, $N = 6$), only the number of species shows a positive correlation with the number of collecting days ($r = 0.82$, $P < 0.05$, $N = 6$). Consequently, this sampling factor cannot alone explain the differences observed between the various multi-species communities. In fact, there are strong differences in their qualitative composition which we think may reflect to some extent the strongly different habitats studied. For instance, at Cape Maclear along the Lake Malawi shoreline, the drosophilid fauna typifies open dry habitats with 6 species of the *Drosophila montium* subgroup (including 4 *bakoue*-like species) out of 11 drosophilid species collected at this locality. At Luwawa on the Vipha Plateau, 8 species of 27 collected belong to the genus *Zaprionus*; these are 8 of the 12 *Zaprionus* species recorded in Malawi including 6 species found at Luwawa only. We presently ignore the ecological rationale, if any, of such unusual and hence unexpected local bias towards increased *Zaprionus* diversity, inasmuch as the

TABLE 3

Check-list and distribution of drosophilid species from Malawi.

* = New species described; ** = New species (left undescribed); + = Cosmopolitan or distribution extending beyond limits of Afrotropical Region; ? = Species assumed to exist in the relevant region (based on known distribution); (x+y) indicates number of species identified (x) or unidentified (y) for the relevant genus; - denotes not recorded. Southern Malawi: 1. Zomba Plateau (790 m); 2. Cape Maclear (500 m). Central Malawi: 3. Lilongwe (1000 m); 4. Kasungu (1040 m). Northern Malawi: 5. Viphya Plateau, Luwawa (1500 m); 6. Nyika Plateau, Chowo (2120 m); 7. Nyika Plateau, Chilinda (2250 m). RSA = Republic of South Africa. SOUTH = South-central African mainland (Zimbabwe, Mozambique, Angola). EAST = East Africa (Kenya, Tanzania). WEST = West-, West-central and Central Africa (from Senegal to Zaïre) plus Atlantic Islands. IO = Indian Ocean Islands, including Madagascar.

GENUS SUBGENUS SPECIES	MALAWI	RSA	SOUTH	EAST	WEST	IO
Amiota (2)						
<i>Amiota</i>						
<i>A. (A.) bandai*</i>	1	-	-	-	-	-
<i>Phortica</i>						
<i>A. (P.) fenestrata</i>	4, 5	+	+	+	?	-
Apenthesia (2)						
<i>Apenthesia</i>						
<i>A. (A.) argyrea*</i>	1	-	-	-	-	-
<i>A. (A.) obscura*</i>	7	-	-	-	-	-
Leucophenga (3+8)						
<i>Leucophenga</i>						
<i>L. (L.) mansura</i>	1	+	+	?	+	-
<i>L. (L.) proxima</i>	5	+	+	+	+	-
<i>L. (L.) subpollinosa+</i>	1, 5	+	-	+	-	-
<i>L. (L.)</i> sp. A**	1	-	-	-	-	-
<i>L. (L.)</i> sp. B**	1	-	-	-	-	-
<i>L. (L.)</i> sp. C**	5, 6	-	-	-	-	-
<i>L. (L.)</i> sp. D**	1	-	-	-	-	-
<i>L. (L.)</i> sp. E**	1	-	-	-	-	-
<i>L. (L.)</i> sp. F**	6	-	-	-	-	-
<i>L. (L.)</i> sp. G**	5	-	-	-	-	-
<i>L. (L.)</i> sp. H**	5	-	-	-	-	-
Stegana (2)						
<i>Stegana</i>						
<i>S. (S.)</i> sp. A	1	-	-	-	-	-
<i>S. (S.)</i> sp. B	5	-	-	-	-	-
Drosophila (25+5)						
<i>Dorsilopha</i>						
<i>D. (Dors.) busckii</i>	+1, 5, 7	+	+	+	+	+
<i>Drosophila</i>						
<i>D. (D.) adamisa*</i>	5	-	-	-	-	-
<i>D. (D.) adamsi</i>	5	+	+	+	+	-
<i>D. (D.) brachytarsa*</i>	3	-	-	-	-	-
<i>D. (D.) buzzatii</i>	3	+	+	?	+	+
<i>D. (D.) hydei+</i>	+	+	-	+	+	+
<i>D. (D.) immigrans+</i>	1, 2, 7	+	+	?	?	+
<i>D. (D.) hirtipes</i>	4	-	-	-	+	+
<i>D. (D.) nasuta+</i>	1	-	+	+	+	+
<i>D. (D.) seyanii*</i>	6	-	-	-	-	-
<i>D. (D.)</i> sp. A aff. <i>seyanii</i>	6	-	-	-	-	-
<i>D. (D.)</i> sp. B aff. <i>seyanii</i>	6	-	-	-	-	-
<i>Sophophora</i>						
<i>D. (S.) bakoue</i>	1, 2, 4	-	-	-	+	-
<i>D. (S.) burlai</i>	1, 2, 5	-	-	+	+	-
<i>D. (S.) curta*</i>	2	-	-	-	-	-

TABLE 3
[Continued]

GENUS SUBGENUS SPECIES	MALAŴI	RSA	SOUTH	EAST	WEST	IO
<i>D. (S.) dentissima</i>	5	+	+	-	-	-
<i>D. (S.) dimitroides*</i>	1	-	-	-	-	-
<i>D. (S.) fima</i>	1, 5	+	+	+	+	-
<i>D. (S.) greeni</i>	1, 2, 4	-	+	-	+	-
<i>D. (S.) ifestia</i>	6, 7	-	-	+	+	-
<i>D. (S.) kivuensis</i>	6	-	-	+	-	-
<i>D. (S.) melanogaster+</i>	1, 3, 4, 5	+	+	+	+	+
<i>D. (S.) neomitra*</i>	1	-	-	-	-	-
<i>D. (S.) seguyiana*</i>	1, 5	-	-	-	-	-
<i>D. (S.) seguyi</i>	1, 2, 4	-	-	-	-	-
<i>D. (S.) simulans+</i>	1, 3, 4, 5, 7	+	+	+	+	+
<i>D. (S.) yakuba</i>	1, 2, 4	+	+	+	+	+
<i>D. (S.) sp. n. aff. phyle**</i>	1	-	-	-	-	-
<i>D. (S.) sp. C aff. seguyi**</i>	5	-	-	-	-	-
<i>D. (S.) sp. D aff. curta**</i>	2	-	-	-	-	-
<i>Hirtodrosophila</i> (1)						
<i>H. vina</i>	6	-	-	-	+	-
<i>Liodrosophila</i> (1)						
<i>L. lampira</i>	6	+	-	-	-	-
<i>Lissocephala</i> (5+2)						
<i>L. couturieri</i>	1	-	-	-	+	-
<i>L. bergi*</i>	1	-	-	-	+	-
<i>L. kamundii*</i>	1	-	-	-	-	-
<i>L. lehou</i>	1	-	-	-	+	-
<i>L. sosefi*</i>	1	-	-	-	-	-
<i>L. sp. A</i>	1	-	-	-	-	-
<i>L. sp. B</i>	4	-	-	-	-	-
<i>Mycodrosophila</i> (2)						
<i>Mycodrosophila</i>						
<i>M. (M.) dudleyi*</i>	6	-	-	-	-	-
<i>M. (M.) nigrans*</i>	6	-	-	-	-	-
<i>Scaptodrosophila</i> (6)						
<i>S. caliginosa</i>	5	+	?	?	+	+
<i>S. dibi</i>	5	+	?	+	+	-
<i>S. lambi</i>	2	-	-	+	+	+
<i>S. latifasciaeformis</i>	1, 2	+	+	+	+	+
<i>S. melaena*</i>	1, 5	-	-	-	-	-
<i>S. smicra</i>	4	-	-	+	+	-
<i>Zaprionus</i> (9+3)						
<i>Zaprionus</i>						
<i>Z. (Z.) camerounensis</i>	3	-	-	-	-	+
<i>Z. (Z.) ghesquieret</i>	1, 2, 3, 4	+	+	+	+	+
<i>Z. (Z.) indianus+</i>	1, 2, 3, 4, 5	+	+	+	+	+
<i>Z. (Z.) proximus</i>	5	-	-	+	-	-
<i>Z. (Z.) sp. B aff. proximus</i>	5	-	-	-	-	-
<i>Z. (Z.) sepsoides</i>	3	+	+	+	+	+
<i>Z. (Z.) spinipilus</i>	5, 7	-	-	+	-	+
<i>Z. (Z.) sp. A aff. spinipilus</i>	1, 5	-	-	-	-	-
<i>Z. (Z.) taronus</i>	5	-	-	-	+	-
<i>Z. (Z.) sp. C aff. taronus</i>	1, 5	-	-	-	-	-
<i>Z. (Z.) tuberculatus+</i>	3	+	+	+	+	+
<i>Z. (Z.) vittiger</i>	5	+	-	-	-	-
Total no of species	76	23	19	24	31	17
Species identified	57	23	19	24	31	17
% common with Malaŵi		40	33	42	54	30

Luwawa forest includes extensive *Pinus* planted areas. On the Nyika Plateau three genera were found which were not recorded anywhere else in Malaŵi, namely *Mycodrosophila*, *Hirtodrosophila* and *Liodrosophila*; these genera are generally expected from tropical rainforests mostly of Guineo-Congolian type. Finally, six of

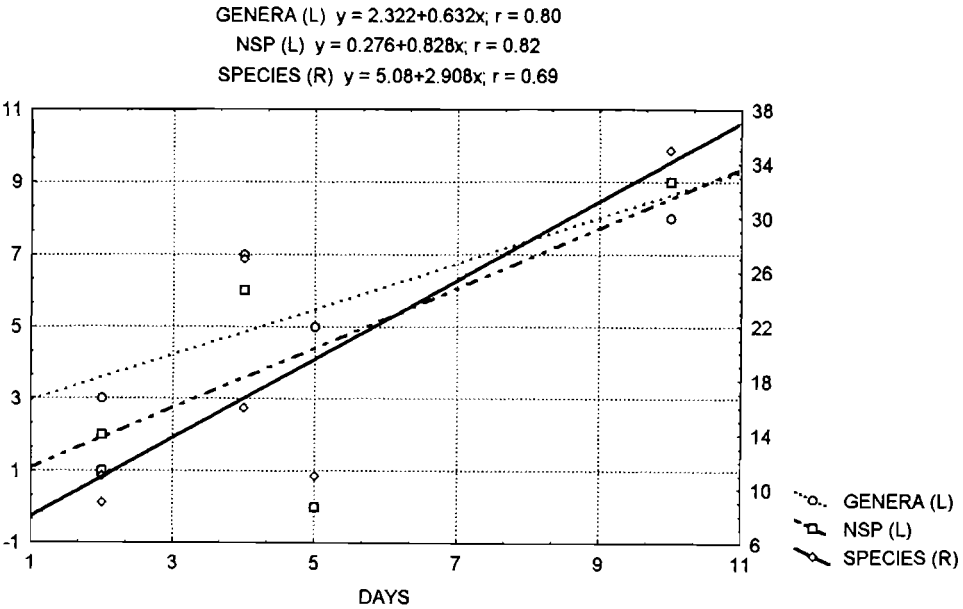


Fig. 102. Relationships between the number of collecting days (abscissa) and the number of genera or new species (left coordinates) or species of Drosophilidae (right coordinate) recorded in Malaŵi. Only the relationship between days of capture and number of species gives a significant positive correlation (solid line).

the seven *Lissocephala* species and two of the three *Drosophila fima* group species recorded in Malaŵi were found only in Zomba town. But, it is clear that this peculiar fauna is not a local peculiarity but relates to the massive fruiting of fig-trees at the time of collection there (see below). Undoubtedly, a diversity of fruiting *Ficus* species from a number of other localions and habitats throughout Malaŵi should provide comparable, albeit not necessarily similar, fig-associated faunas. This points to the importance of plant-drosophilid assemblages in tropical Africa. Unlike domestic and cosmopolitan species (e.g. *D. melanogaster*, *D. simulans*, *D. busckii*, *D. immigrans*, *D. nasuta*), the overwhelming majority of the afrotropical species of Drosophilidae have specific requirements for breeding. A number of genera and species groups are involved in wide radiations in association with a diversity of host-plants. Some of these radiations are illustrated in Malaŵi.

TABLE 4
Synopsis of current data on Drosophilidae of Malaŵi.

Species previously known	40	52.6 %
Species grouped, likely known but unidentified	15	19.7 %
Species new, here described	16	21.0 %
Species suspected to be new, but left undescribed	5	6.6 %
Total	76	100 %

Radiation of *Lissocephala* and *fima* group species on *Ficus* (Moraceae)

A special focus of the field work in Malaŵi was on Drosophilidae associated with tropical African figs, and this accounts for the 10 strictly fig-breeding species recorded here. Two independent major radiations have occurred on figs, that is on the syconial receptacles (cryptic inflorescences/infrutescences) of the genus *Ficus* (Moraceae), in the Afrotropical Region (Lachaise *et al.* 1982). One concerns the species of the genus *Lissocephala* (23 spp.), the other those of the *Drosophila fima* group (17 spp.). The former breed in the syconial cavity of developing figs (i.e. green immature syconia), the latter in very ripe decaying figs on the ground (i.e. dark red and black syconia). Thus, *Lissocephala* exploit figs at a time when other drosophilids do not, while *fima* group representatives use the same resource when other drosophilid species no longer use it. Inbetween, that is during late male floral phasis on the fig-tree and early postfloral phasis on the ground corresponding to the fig seed disperser attraction (i.e. red/yellow sugary fleshy syconia), is a *window* that is a resource suitable for a number of opportunistic insect species including a diversity of drosophilids. A clear distinction should be made between these opportunistic facultative fig feeders/breeders and those obligatory fig-breeding specialists involved in the radiations on *Ficus*. In the present survey, 24 such opportunistic drosophilid species (including 6 genera) were caught on fallen figs, mostly at Zomba. But, attention will henceforth be directed solely to the 10 strictly fig-breeding species recorded in Malaŵi.

Of a total of 28 fig-tree species reported from Malaŵi (Berg 1990a), 12 were recorded during the field trip (Berg, *pers. comm.*; Lachaise, *unpubl.*). Although a few species were found in early fruiting (e.g. *Ficus abutilifolia* at Cape Maclear, and *Ficus ingens* on Thumbi West Island, both on Lake Malaŵi rocky shorelines; *Ficus stuhlmannii* in Kasungu National Park, *Brachystegia* woodland; *Ficus sur* at Luwawa Forest Reserve along Luwawa Pond on the Viphya Plateau), only two – *Ficus sycomorus* and *F. thonningii* from Zomba – provided a significant crop and therefore diversity (10 spp.) of obligatory fig-breeding drosophilids. One unidentified *Lissocephala* female was also recorded from *Ficus thonningii* figs at Kasungu, and four *Drosophila fima* individuals in Luwawa forest, a record that is most likely relevant to the presence of fruiting *Ficus sur* near Luwawa pond.

A collection of 151 *Lissocephala* specimens were collected during field work. Interestingly, there was a clear host-plant divide on two sympatric fig-tree species, namely *Ficus sycomorus* and *F. thonningii* of which fruitings overlapped. The former yielded three new species of *Lissocephala* (*bergi*, *kamundii*, *sosefi*) which were not found on the latter. Moreover, a fourth species (*L. couturieri*) had 96 % of its abundant population on *F. sycomorus* and only 4 % on *F. thonningii*. However, two other species, *L. lebou* and *Lissocephala* sp. A, were found on *F. thonningii* alone. Of note is the observation that *L. bergi*, *L. sosefi* and *L. lebou* had females with a medium length telescopic postabdomen while *L. couturieri* had females with a long telescopic postabdomen. These features are consistent with the adaptive syndromes (suites of coordinated morphological and behavioural traits) expected from *Lissocephala* species exploiting syconia in the male phasis. The length of the postabdomen allows the female to lay eggs deep into the tunnel bored by the males of

the new generation of agaonid fig wasps for their females to escape (Lachaise & McEvey 1990). In fact, the above-mentioned two fig-trees which were a few hundred metres apart, differed in that the former had thousands of figs mostly in the interfloral and male phases, while the latter had hundreds of figs in the male and postfloral phases, mostly fallen onto the ground. Consistent with the developmental stages of the figs of both *Ficus* species studied at Zomba, there were no representatives of those *Lissocephala* with short-postabdomened females which are known to exploit figs much earlier at the female phasis by laying eggs in the ostiole (Lachaise 1977). Concerning biogeography, *L. kamundii* and *L. sosefi* have as yet been reported only from East Africa (Malaŵi). In contrast, *L. couturieri*, *L. lebou* (Harry *et al.* 1996), and the new species *L. bergi* have been recorded in both East and West Africa.

TABLE 5

Biogeographic affinities of the Drosophilidae of Malaŵi (based on 56 identified species only). RSA = Republic of South Africa; SOUTH = South-central African mainland (Zimbabwe, Mozambique, Angola); EAST = East Africa (Kenya, Tanzania); WEST = West-, West-central and Central Africa (from Senegal to Zaïre) plus Atlantic Islands; IO = Indian Ocean Islands, including Madagascar.

Eastern		
<i>Confined to east of the Rift, not extending south of the Limpopo River, also in IO</i>		
New species described, presumed to be endemics	16	33.9 %
Species: Malaŵi + EAST	2	
Species: Malaŵi + EAST + IO	1	
Southeastern		
<i>Not on western mainland</i>		
Species: Malaŵi + EAST + IO + SOUTH + RSA	1	
Species: Malaŵi + IO + SOUTH + RSA	1	10.7 %
Species: Malaŵi + EAST + RSA	1	
Species: Malaŵi + SOUTH + RSA	1	
Species: Malaŵi + RSA	2	
Western-Southern		
<i>Not on northeastern mainland</i>		
Species: Malaŵi + SOUTH + RSA + WEST	1	3.6 %
Species: Malaŵi + SOUTH + WEST	1	
Western-Eastern		
<i>Not on southern mainland</i>		
Species: Malaŵi + WEST	7	
Species: Malaŵi + WEST + IO	1	21.4 %
Species: Malaŵi + EAST + WEST	3	
Species: Malaŵi + EAST + IO + WEST	1	
Widespread		
Species: Malaŵi + EAST + IO + SOUTH + WEST	1	
Species: Malaŵi + IO + RSA + WEST	1	30.4 %
Species: Malaŵi + EAST + SOUTH + RSA + WEST	4	
Species: Malaŵi + EAST + IO + SOUTH + RSA + WEST	11	
Total	56	100 %

With regard to the *Drosophila fima* group species, the discovery of two new species (*dimitroides* and *neomitra*) on late decaying tannin-loaded figs is consistent with previous data on this highly homogeneous taxonomic-ecological species group. The occurrence of the species *D. fima* on both *Ficus sycomorus* and *F. thonningii* is

also consistent with the fact that among the *fima*-like species it is the least specialised (i.e. breeding also in early decaying figs and a few extra resources). However, from these additional observations on increasingly numerous species of the *fima* group, the question arises as to how these taxonomically and ecologically related species can coexist. In fact, these species exemplify the opposite of competitive displacement. This speciose group illustrates rather the paradox of specialist species packing (mix of closely related species with marked ecological similarity) which we have long emphasised but not explained (Tsacas & Lachaise 1981, Lachaise & Tsacas 1983).

Radiation of *Apenthecia* on *Aloe* (Liliaceae)

Following Tsacas (1983), there is growing evidence that within *Apenthecia* (11 spp.), the subgenus *Apenthecia* is endemic to the eastern and southern African mainland (10 spp.). The two new species found on the Zomba and Nyika Plateaux respectively in Malawi are of interest as they elucidate the extent of speciation events and the biogeographical range of that taxon closely associated to *Aloe* and possibly *Aloe*-like host-plants. Importantly, they fill the gap in south-central Africa between records in South Africa (from KwaZulu-Natal to the Cape) to the south and Kenya to the north.

TABLE 6

Flowering seasons of plant species visited by sunbirds on the Nyika Plateau (after Dowsett-Lemaire, 1989b). Drosophilidae of the genus *Apenthecia* are closely associated with *Aloe* and presumably *Kniphofia* (Liliaceae).

Plant species	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
<i>Kniphofia linearifolia</i>	•	•	•	•		•						
<i>Kniphofia grantii</i>	•	•	•	•	•	•						
<i>Aloe nuttii</i>						•	•					
<i>Aloe mzimbana</i>							•	•	•			

Although the Malawian records were not made directly on *Aloe*, they are most likely relevant to the 16 local *Aloe* species, all of which are native (D. A. Kamundi, pers. comm.). Relevant to the very Chancellor College site at Zomba where *Apenthecia argyrea* was caught, the sympatric *Aloe* species were: *Aloe arborescens* Mill.; *Aloe chrytopoda*; *Aloe duckeri* Christian; *Aloe excelsa* Berger; *Aloe greatheadi* Schnol; *Aloe mavii* Christian; *Aloe myriacantha* (Haw) Roem & Schult. Noteworthy also is *Aloe mzimbana* Christian, which may not be cultivated but *in situ* there. On the Nyika Plateau at 2250 m, where *Apenthecia obscura* was caught, two species of *Aloe* are reported, namely *Aloe nuttii* and *Aloe mzimbana*. These two species provide suitable resources for *A. obscura*, but only from April to July (Table 6 after Dowsett-Lemaire 1989b). The question then arises as to which resource sustains the *Apenthecia* population over the eight remaining months. A possibility is that they also breed in inflorescences of the allied genus *Kniphofia*. The two genera *Aloe* and *Kniphofia* belong to two subfamilies (Aloioideae and Asphodelideae respectively) in the same small family (Liliaceae/Asphodelaceae). They have similar floral and pollination structures, although the leaves are succulent in *Aloe* alone. On the Nyika Plateau the two *Aloe* species and two *Kniphofia* species, *K. linearifolia* and

K. grantii, were shown to flower consecutively during the annual cycle, thereby providing continuous potential breeding sites from November to July (Table 6). However, evidence that *Kniphofia* is actually exploited as a drosophilid resource is still lacking, and it needs to be explained how the three month gap between August to October is overcome.

Radiation of *Scaptodrosophila aterrima* group species on Tubiflorales

Wherever they live, the *aterrima* species group of *Scaptodrosophila* is invariably associated for breeding with short-lived tubular flowers, mostly of Malvales and Tubiflorales. For example, they use predominantly flowers of *Hibiscus* and *Ipomoea* which belong to the families Malvaceae and Convolvulaceae respectively (Lachaise *et al.* 1983, Tsacas *et al.* 1988). *Scaptodrosophila smicra* Tsacas, 1980, is a widespread species previously reported from Mt Nimba in Guinea-Ivory Coast, Brazzaville in Congo and from Mt Elgon in Kenya. Its geographical range appears now to extend to the south-central African mainland. In Malawi, at the Kasungu Lodge, this species is commonly found by the edge of the Lifupa pond in flowers of *Hibiscus panduriformis* Burm. f., where it breeds. In Congo, *S. smicra* is reported to breed in flowers of *Hibiscus esculentus* L.; on Mt Nimba it was recorded at 1415 m in the submontane grassland where *Hibiscus asper* Hook. f. was formerly reported (Schnell 1952). *Scaptodrosophila caliginosa* Lamb, recorded on the Viphya Plateau in the Luwawa forest reserve, is widespread throughout the African mainland, and occurs from the Cape Verde Islands in the far northwest, to the Seychelles in the east, and to Madagascar and Mauritius in the southeastern limit of its range. *S. caliginosa* was recorded from *Hibiscus esculentus* L. in Senegal and Ivory Coast, from *H. cannabinus* L. in Ghana, and from *Ipomoea* spp. in Seychelles, Madagascar and Mauritius. Additional breeding sites include Cucurbitaceae flowers in Congo, Seychelles and Mauritius, *Sparmannia* (Tiliaceae) flowers in Congo, and flowers of *Lilium* sp. (Liliaceae) in Nigeria.

Sister species of the *aterrima* species group were shown to exploit flowers of *Gossypium* (Malvaceae), *Merremia* (Convolvulaceae), *Datura* (Solanaceae), *Canna* (Cannaceae) and *Cryptostegia* (Asclepiadaceae), in addition to a diversity of *Hibiscus* and *Ipomoea* (Tsacas *et al.* 1988). Thus the records from Malawi fully support the conclusion that the *Scaptodrosophila aterrima* group species are restricted to flowers for breeding. More generally the flower-breeding *Scaptodrosophila* exploit large attached tubular flowers. The tubular Malvale flower pattern typifies the most suitable breeding site in the Afrotropical Region. Some 20–40 adult flies were found per *Hibiscus panduriformis* flower at Kasungu in Malawi. Larvae breed in decayed flowers.

Interestingly, flower-breeding *Scaptodrosophila* of other species groups were consistently reported from *Hibiscus* in Australia and the Nearctic Region (Cook *et al.* 1977), and from *Malvaviscus* (Malvaceae) and *Ipomoea* in Singapore (Okada 1975). Moreover, the genus *Scaptodrosophila* was shown to have exhibited a major adaptive radiation into a diversity of the flower breeding niches, especially *Phaeomeria* (Okada & Nishiharu 1981), *Colocasia* and *Alocasia* (Araceae), *Thunbergia* (Acanthaceae), *Datura*, *Hibiscus*, *Ipomoea*, and two leguminous vines – *Mucuna* and

Strongylodon – in Papua New Guinea (Carson & Okada 1980, Okada & Carson 1980 1982a,b). The high diversity of drosophilid species of various species groups in different biogeographic regions and the array of host-plant families exploited, including both Monocotyledonae and Dicotyledonae, suggests that the inflorescence-breeding habit is an ancestral trait within the genus *Scaptodrosophila*. The problem is very similar to that concerning the ecological consistency of the *Drosophila fima* group species mentioned above. In support of the antiquity of the inflorescence-dependent life history, are possibly the adaptive radiations of the Oriental-Australasian-Afrotropical *brunnea* species group Tsacas & Chassagnard, 1976, and of the Afrotropical *saba* species group Burla, 1954, on palms (Burla 1955, Lachaise & Tsacas 1983, Tsacas *et al.* 1988), and of the Australasian *brunneipennis* Bock & Parsons, 1978, species group on ferns (Bock & Parsons 1978). Both palms and ferns may be elements derived from a remote Gondwanian flora. Consistently, the flower-breeding feature may have been a trait of the ancestral *aterrima* stock.

The fungus-dependent genera

The genus *Hirtodrosophila* is poorly represented in Africa and there is only one species – *H. vina* Burla, 1954 – in the Malaŵi collection. On the Nyika Plateau, it is nonetheless not rare; about 40 individuals were collected by sweeping close to standing trunks covered by fungi. The Chowo forest on the Zambian border of the Nyika Plateau was remarkable for the abundance of fungi growing on dead standing trunks at the head of the valley, where mosses and ferns are also abundant. This *Hirtodrosophila* species appears closely associated with fungi. In Ivory Coast it was consistently recorded on fungus in both Banco forest Reserve and M'Bettie forest. Its vernacular djoula name 'vina' means 'fungus' (Burla 1954). The same ecological observations were made in Congo. The claw-like ovipositor of *H. vina* (typical of the *Hirtodrosophila hirticornis* species group) strongly suggests consistent ecological requirements. Half the collection of that species from Nyika was devoted to the analysis of amylases which appear to present peculiar genetic and molecular features in fungus-breeding drosophilids (Cariou & Prigent, *in prep.*).

The role of fungi as a major resource for Drosophilidae on the cold Nyika Plateau is further testified by the discovery in the Chowo forest of two new strictly fungus-breeding species of *Mycodrosophila*, *M. dudleyi* and *M. nigrans*, described above. Two representatives of the genus *Leucophenga* were also shown to live sympatrically in this forest patch. Although the association of these two *Leucophenga* species with fungi is still uncertain, it is of interest to note that a great deal of afrotropical *Leucophenga* were shown to breed on that resource. Nevertheless, there are four species groups of *Leucophenga* in Malaŵi, two on the Nyika (represented by the two sympatric Chowo species), three on the Viphya Plateau (five species) and all four on the Zomba plateau (six species), and these species groups may include various arrays of ecological patterns. The multi-species community of fungus breeders (*Hirtodrosophila*-*Mycodrosophila*-*Leucophenga*) living in the dark forest patches of the Nyika is reminiscent of those living in temperate holarctic areas.

The invaders/colonisers

Among the cosmopolitan and domestic species, *D. nasuta* is generally assumed to replace in the paleotropical zone (David & Tsacas 1981) its sister species *D. immigrans*, which occurs in the Palearctic-Middle East area. Curiously, in Malaŵi both species are recorded sympatrically at Zomba. Intriguingly, the opportunist *Scaptodrosophila latifasciaeformis* which is prone to change rapidly from one resource to another (Lachaise 1983) seems quite rare in Malaŵi, and the invading *Drosophila malerkotliana* remains unrecorded from the present collection. This is puzzling since both can reach considerable population sizes elsewhere, especially in West Africa. The depauperate subgenus *Dorsilopha* comprises four species of which three are restricted to Burma (Toda 1986). Only the fourth and cosmopolitan species, *D. busckii*, was previously reported from the Afrotropical Region, and it was found in Malaŵi. There are very poor affinities between the southeastern African mainland and the Nearctic Region. One is however, *Drosophila buzzatii*, a basically cactiphilic species of the *Drosophila repleta* species group. Growing evidence indicates that this species extended its geographical range as an *Opuntia*-stowaway. The *Drosophila* species appears to exist throughout the entire *Opuntia* distribution. Maintenance of populations is dependent on cladode rots (Barker 1982, Murray 1982).

The montane species of the *Drosophila dentissima* group and the Nyika-Viphya limit

The *dentissima* species group includes 16 montane species (Tsacas 1980*b*). The group is of major interest for understanding the connections between the mountain ranges of the East African highlands and more distant ones further west and south. It is represented in Malaŵi by two species, *D. dentissima* and *D. kivuensis*. *Drosophila kivuensis* was formerly found in the Virunga and Ruwenzori Ranges (1790–2324 m). Its discovery in the Chowo forest (2120 m) on the Nyika Plateau indicates that its range extends not only over the Western Border Range but southwards into northern Malaŵi. Uplift of the huge block of Precambrian rocks of the Ruwenzori Range in the Zaïre-Uganda border area occurred mainly in the Pliocene, while the Virunga volcanoes northeast of Lake Kivu and the Rungwe volcano at the head of Lake Malaŵi were built up later in the Pleistocene (Griffiths 1993). These geological considerations and the highest diversity of the *dentissima* relatives on the Western Border of the Rift, suggest that *D. kivuensis* has a northern origin and expanded its range southwards. Consistent with this is a sister species, *D. vumbae*, which occurs further south in the eastern escarpment forests of Zimbabwe on Mount Vumba at 1500 m (Bock & Wheeler 1972), Mount Nyangani at 1920 m, and Mount Chimanimani at 1550 m in the *Uapaca* formation (new records, February 1997, Lachaise & Harry, *unpubl.*). Whether *D. kivuensis* and *D. vumbae* are vicariant or result from a stepping-stone migration and differentiation is controversial. The finding of *D. dentissima* at 1500 m on the Viphya Plateau in the Luwawa forest is in this respect worth noting. This species is closely related to *D. kivuensis* and *D. vumbae*. Paradoxically, *D. dentissima* was only known so far from South Africa. There, it was reported from riverine forest or bush in the Drakensberg at an elevation similar (1540 m) to that on the Viphya Plateau. However, it was also found in the

Cape Province in coastal lowland forests below 100 m. This distributional pattern suggests that *D. dentissima* has a northern origin and was originally a montane species, but its wider ecological tolerance allowed it to spread to lower altitudes and to expand its range to the south where temperate and seasonal conditions were suitable. Of major interest is that the three sister species: *D. kivuensis*, *D. dentissima* and *D. vumbae*, have non-overlapping geographical ranges and the limit between those of the two former species is in Malawi between the Nyika and Viphya Plateaux. The Nyika highlands have more connections with the Western Border Range to the northwest of Lake Tanganyika, and the Viphya highlands with southern mountain ranges. In general, it is worth emphasising that the *dentissima* species group also shows connections between East African mountains and Cameroun. There are a series of sister species in diverse species complexes within the *dentissima* species group in the Eastern highlands and Cameroun respectively (Tsacas 1980).

The Nyika Plateau reveals Madagascan and Oriental links

Drosophilidae provide a few interesting indices supporting the antiquity of the evergreen forest on the Nyika Plateau. Currently, 2–4 % of the plateau area is covered by indigenous evergreen forest. The history of the plateau vegetation is controversial. Some authors argue that the small 1–2 acre patches are relicts of an extensive moist evergreen forest once covering most of northern Zambia, Malawi, Mozambique and southern Tanzania (Chapman & White 1970). However, pollen analysis suggests the existing proportion of grassland to forest has changed little over the last 11000 years (Meadows 1984). This author stressed that between 20000 and 12000 years ago the climate became drier than at present and less favourable to the moist evergreen forests; drier conditions also favoured fire, to which the forest was highly susceptible, leading to a progressive decline of forest cover. Forests are now mostly found in moist hollows or valley heads and occasionally in steep rocky areas inaccessible to fire (Dowsett-Lemaire 1985, 1989c). The Chowo forest is one such evergreen forest patch. Although only a very short time could be devoted to drosophilid collecting there, it provided a most interesting small sample, suggesting surprising biogeographic affinities.

The new species of the *robusta* group, *Drosophila seyanii*, is of major interest as it represents the first afrotropical record of a member of this basically oriental (there is only one nearctic and one palearctic species) species group. This unexpected find provides further evidence of relationships between the oriental and afrotropical drosophilid faunas. The question arises as to whether *D. seyanii* should be considered as suggesting old affinities with the Oriental Region, or a recent migration? The finding in the Chowo forest of two pairs of females which might belong to two more species of the *robusta* group (unequivocal assignment would require males), supports the former hypothesis. In support of the antiquity of the Nyika Plateau forest is probably also the finding in the Chowo forest patch of *Liodrosophila lampra*, a species previously known from the Chirinda forest in eastern Zimbabwe and the Dhlinda forest (near Eshowe, Kwa-Natal, South Africa). The genus *Liodrosophila* is represented in the Afrotropical Region by seven species (four from East Africa): *L. lucida* (Séguy, 1938) and *L. melania* (Séguy, 1938) on Mt Elgon in Kenya at 2400 m

and 2470 m respectively, *L. argyrea* Tsacas, 1990, in KwaZulu-Natal where it is sympatric with *L. lampra* in the Dhlhlinza forest, three species from Madagascar (*L. divergens* Okada, 1974, *L. madagascariensis* Okada, 1974, and *L. sinuata* Okada, 1974) and one new undescribed species close to *L. sinuata* in Comoro (Tsacas, *unpubl.*). It clearly indicates a link between southeastern Africa and Madagascar via the Comoro archipelago. However, we report here new localities for the genus in Ivory Coast, Nigeria, Central African Republic, Cameroun and Gabon. Wherever they are found in the afrotropics, representatives of the genus *Liodrosophila* are fairly rare and locally confined. Therefore, it can be assumed that they are sedentary species not prone to long-range dispersal. Consistent with this is the absence of *Liodrosophila* from both the Mascarene and Seychelles islands. However, considering that the genus *Liodrosophila* is highly diversified in the Oriental Region, it is uncertain that afrotropical relatives arose from oriental stock.

Montane links between eastern/southeastern Africa and western Cameroun

Drosophila (*D.*) *brachytarsa* belongs to the subgenus *Drosophila*. The species collected at Lilongwe in central Malaŵi was previously reported from Zaïre (Upemba National Park by the Lusinga River and tributary, near Mukana), and from Mahali (Makari) in Tanzania at 1829 m on the southeastern edge of Lake Tanganyika. It was also reported from Kenya on Mt Elgon at 2880 m, in *Podocarpus* forest and on red fallen fruits of *Rhamnus prinoides* L'Hérit. (Rhamnaceae). This small tree is an afromontane, near-endemic species (Dowsett-Lemaire 1990) occurring occasionally in submontane forests of 1970–2200 m or frequently on the High plateau like Nyika between 2250 and 2450 m (Dowsett-Lemaire 1985). Of note is the occurrence of an undescribed new species near *brachytarsa* at Bafut N'gemba, Mt Lefo, at about 2000 m on the Bamiléké Plateau (Bamenda-Banso block) in west Cameroun (Tsacas, *unpubl.*). *Drosophila brachytarsa* is also closely related to *D. ponera*, which was found in the Cameroun mountains (new record), and at 400 m on Réunion island (David & Tsacas 1975). Unlike *D. brachytarsa*, neither the new species near *brachytarsa* nor *D. ponera* has as yet been proved to be associated with *Rhamnus prinoides*. It is nevertheless of note that this *Rhamnus* species is common between 1800 and 2050 m on the Bamenda-Banso block in Cameroun, and is widespread in montane woodland and margins of montane forest from Abyssinia to Angola and South Africa (Hutchinson & Dalziel 1954); the range of *D. brachytarsa*-related species in the afrotropics may relate to such groups of afromontane plants.

CONCLUSION

This study of the drosophilid fauna of Malaŵi fills a longstanding gap in our knowledge of the family on the southeast African mainland. The species composition indicates that Malaŵi stands at the crossroads between east, south and west. A characteristic feature of the ecological relationships of the Malaŵian, and more generally afrotropical, drosophilids, is the consistency with which members of a particular taxon (genus *Mycodrosophila* on fungus, genus *Apenethecia* on *Aloe*, genus *Lissocephala* on green figs, *Drosophila fima* species group on red-black figs, *Scaptodrosophila aterrima* species group on Tubiflorales) use the same breeding substrate. In view of this data set

we concur with Kambysellis *et al.*'s (1995) conclusion made for Hawaiian *Drosophila* based on molecular versus ecological evidence, that ecological shifts occurred very early in the initial phyletic diversification of the relevant groups. The association of *Mycodrosophila* with fungus is certainly very old, this occurring throughout the world. As far as we know there are no non-mycophagous *Mycodrosophila*. Concerning the genus *Scaptodrosophila* it was argued above that although there are species groups which do not use flowers as a breeding niche, the ancestor was most presumably a flower-breeder. A peculiar feature of African drosophilids is the use of the same part of the same plant (*Ficus* spp.), namely the fig receptacles (syconia), by two unrelated taxa (i.e. the genus *Lissocephala* and the *Drosophila fima* species group), at two times during the inflorescence development.

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